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Research Document 2004/128 | Document de recherche 2004/128

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A review of biological principles and methods involved in setting minimum population sizes and recovery objectives for the September 2004 drafts of the Cultus and Sakinaw Lake sockeye salmon and Interior Fraser coho salmon recovery plans

Examen des principes et des méthodes biologiques utilisés pour fixer les effectifs minimums des populations dans les ébauches de septembre 2004 des plans de rétablissement du saumon rouge des lacs Cultus et Sakinaw et du saumon coho de l'intérieur du Fraser

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ISSN 1499-3848 (Printed / Imprimé)
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Abstract

The purpose of this paper is to review the scientific basis for the recovery objectives contained in the September 2004 draft recovery plans for Cultus and Sakinaw Lake sockeye salmon and Interior Fraser coho salmon. First, a brief review of recovery objectives for a variety of other North American salmonid recovery plans was conducted, and we concluded that the objectives of the 3 plans were consistent with current practice; the main difference was that the objectives were more quantitative than was usual in other jurisdictions. Next, objectives that were developed for purpose of conserving genetic resources in the endangered populations were compared to the recent literature and were found to be minimally adequate. In a review of population viability analysis (PVA) and its application to setting conservation targets, we concluded that demographically-based conservation goals in the order of 1,000 annual spawners was only adequate if there was an additional objective of maintaining positive population growth. We detailed and reviewed the evidence for depensatory mortality in Cultus Lake on juvenile sockeye salmon and concurred with the recovery team that there was reason to be concerned that at low spawner abundance reduced smolt production rates could inhibit recovery. Lastly, we documented the evidence used to develop a total escapement estimate for Interior Fraser coho salmon that would meet recovery objectives for individual populations and sub-populations.

A comparison of the recovery objectives with recent historical abundances indicates that the recovery targets for the 3 salmon populations are all less than one third of recent maxima. Thus the teams have been consistent in interpreting recovery as an abundance at the lower range of the spectrum of values they might have considered, well below the carrying capacity of their habitats. We conclude that there is a need to develop plans to maintain population productivity to ensure persistence at the proposed recovery targets.

Résumé

Le but du présent document est d'examiner le fondement scientifique des objectifs de rétablissement présentés dans les ébauches de septembre 2004 des plans de rétablissement du saumon rouge des lacs Cultus et Sakinaw et du saumon coho de l'intérieur du Fraser. Nous avons d'abord effectué un bref examen des objectifs de rétablissement présentés dans une gamme de plans de rétablissement d'autres salmonidés d'Amérique du Nord et nous avons conclu que les objectifs des trois plans sont conformes aux pratiques en vigueur, la principale différence étant que ces objectifs sont plus quantitatifs que ceux dans les plans d'autres autorités compétentes. Ensuite, nous avons analysé les objectifs qui ont été fixés aux fins de conservation des ressources génétiques dans les populations en voie de disparition en fonction des résultats publiés dans des ouvrages récents et nous avons constaté que ces objectifs sont tout juste adéquats. Un examen de la méthode d'analyse de la viabilité des populations et de ses applications liées à l'établissement de cibles de conservation nous a permis de conclure que les objectifs de conservation de l'ordre de 1 000 géniteurs par année ne sont adéquats que si un objectif supplémentaire de maintien d'un taux de croissance positif des populations est fixé. Nous avons présenté de façon détaillée et passé en revue les données sur la mortalité dépensatoire des saumons rouges juvéniles du lac Cultus et nous partageons l'avis de l'équipe de rétablissement selon lequel il est justifié d'être préoccupés par le fait qu'en cas de faible abondance des géniteurs, un taux réduit de production de smolts pourrait empêcher tout rétablissement. Finalement, nous avons rassemblés les données utilisées pour effectuer une estimation de l'échappée totale de saumon coho de l'intérieur du Fraser qui respecterait les objectifs de rétablissement pour les populations et sous-populations individuelles.

La comparaison des objectifs de rétablissement avec les données récentes sur l'abondance révèle que les cibles de rétablissement pour les trois populations de saumons sont toutes inférieures au tiers des maximums récents. Par conséquent, les équipes ont faire preuve d'uniformité lorsqu'elles ont interprété le rétablissement comme étant une abondance près de la limite inférieure de la gamme de valeurs possibles, bien en deçà de la capacité de charge des habitats. Nous concluons qu'il est nécessaire d'élaborer des plans pour le maintien de la productivité des populations afin d'assurer la durabilité aux cibles de rétablissement proposées.

105-06159/

Introduction

Three populations of Pacific salmon (Cultus sockeye, Sakinaw sockeye, and Interior Fraser coho) were deemed designatable units (DU) and listed as *Endangered* in 2002 by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC). A recovery team was appointed for each DU in 2003, and draft recovery strategies were completed by September 2004. These draft strategies are being used for public consultations and review, prior to a final decision on whether to legally list these populations as "wildlife species" under the Species At Risk Act (SARA).

Recovery strategies contain background on the biology of the populations and their significance to society, the status of their habitats and the threats to their persistence. As directed, each recovery team developed a broad-based recovery goal and a series of more specific recovery objectives. Some of the objectives contain numerical targets for population size, while others deal with the threats, institutional arrangements and other items deemed necessary for recovery. To promote consistency in the recovery strategies, some team members served on 2 different recovery teams, and a regional Salmon Recovery Steering Committee was formed to provide guidance to the teams.

The purpose of this working paper is to review specific aspects of the recovery objectives of the three recovery strategies. The objectives agreed upon by each team will reflect the team's analysis of the scientific literature, available population-specific data, and other considerations including the need to reach some form of consensus. It is not the intention of this paper to chronicle each team's decision-making process, but rather to review the recovery objectives with respect to the relevant scientific information.

The *Request for Working Paper* contained the following objective and questions to be addressed:

"Develop a technical background document that identifies the biological principles and methods involved in setting minimum population sizes and the determination of safe levels of recovery to provide guidance for current and future recovery teams."

Specific questions to be addressed:

1. What is the scientific basis for the minimum population sizes required to achieve the genetic integrity of the salmon populations?
2. What is the scientific basis for setting abundance targets intended to achieve recovery?
3. What is the scientific basis for minimum population sizes required to address demographic issues such as depensation or predator pits as identified in Cultus Objective 3, Bullet 3?
4. What is the scientific basis for setting generational average escapement for Interior Fraser coho unit as a whole and at the population and subpopulation levels?"

Our approach is to first briefly review some recent recovery plans for other salmonid fishes to evaluate whether the recovery objectives outlined in the 3 plans are similar in type and rigour to other recovery efforts. Then, we address the 4 questions listed above by reviewing the relevant science, and presenting some of the background analyses that led to the development of the recovery objectives. We then provide some analysis and commentary on those recovery objectives in relation to the available science and data.

Recovery Objectives in other Salmonid Recovery Plans.

To set the stage for this analysis we first review other salmonid recovery plans and describe relevant recovery objectives. The many US Endangered Species Act (ESA) recovery plans can be found at http://ecos.fws.gov/tess_public/TESSWebpage. Canadian plans will be available at http://www.sararegistry.gc.ca/plans/default_e.cfm. Appendix A in this report contains the goals and objectives of the 3 salmon plans.

Inner Bay of Fundy Atlantic salmon: The Inner Bay of Fundy (iBoF) Atlantic salmon DU is the only anadromous (or marine) fish "species" legally listed as *Endangered* in Canada. It comprises populations historically found in about 40 rivers, which collectively may have numbered 40,000 spawners. The populations are now at very low levels (<100 in 2003, Gross and Robertson 2004). The iBoF Atlantic salmon recovery plan (final draft 2002) predates guidelines developed under SARA and is now considered "non-compliant" (L. Marshall, DFO, Halifax). Short term objectives are:

i) To harbour and protect what remains of the residual populations;
ii) To quantify and characterize the freshwater habitat available to restoration;
iii) To identify the number, composition and size of populations essential to restoring stability to the iBoF lineage of Atlantic salmon;
iv) To identify and correct or mitigate the factors preventing or limiting recovery;
v) To restore self-sustaining populations representative of the two principal population groups (i.e., Chignecto and Minas) and of the Gaspereau River;
vi) To monitor and assess progress annually;
vii) To evaluate progress towards population self-sustainability in 2010; and
viii) To involve governments, stakeholders, industry and the general public in the delivery of the Recovery Program.

The plan states that over the long-term, the objective is to restore self-sustaining populations of iBoF salmon throughout the iBoF, where technically feasible and on a prioritized basis. Progress towards this objective will be measured by the number of rivers in which self-sustaining populations of iBoF salmon are re-established. The restoration of iBoF salmon to the 24 rivers in which they were known to be present in 1989 (i.e., immediately before the onset of the decline that has occurred), is proposed as an intermediate milestone to restoring salmon to all iBoF rivers.

No specific abundance targets are provided.

Gulf of Maine Atlantic salmon: There are 8 salmon-producing rivers in this region at the time of listing and the total aggregate abundance is <100 spawners. The June 2004 draft contains three objectives:

1. Halt the decline and demonstrate persistent population growth via 2 criteria:
    a. Spawners present in all 8 rivers
    b. Generational replacement rate >1
2. Achieve conditions necessary for self sustainable populations
3. Ensure threats are diminished and remain so for long-term viability.

Preliminary delisting criteria have been identified as:

1. Population demographics including abundance, structure and distribution such that endangerment is not likely in the near future. This will be informed by modelling results.
2. Stable or increasing population trends.
3. Control of threats

The recovery plan provides no numerical values for delisting criteria 1, but notes that a detailed population viability analysis (PVA) model has been developed and will be used to develop specific targets. Specific delisting criteria will be developed within 3 years after finalization of the plan.

California coho salmon: A recovery plan was finalized by the State of California in June 2004 (http://www.dfg.ca.gov/nafwb/cohorecovery/RecoveryStrategy.html). The plan covers a large area consisting of 2 Evolutionary Significant Units (ESUs) and many streams that historically supported coho salmon. Abundance has declined by 85 to 94% in the past 60 years. The relevant recovery goals (which are similar to 'objectives' in other plans) are:

1. Maintain and improve the number of key populations and increase the number of populations and brood years of coho salmon.
2. Maintain and increase the number of spawning adults.
3. Maintain the range and maintain and increase the distribution.
4. Maintain existing essential habitat for coho salmon
5. Enhance and restore habitat within the range of coho salmon.
6. Reach and maintain coho salmon population levels that allow for the resumption of fisheries. (this objective was not part of recovery, as defined by legislation).

The process for deriving delisting criteria for each of the goals is outlined in the plan. First, the 2 ESU's were divided into 'recovery units' which generally corresponded with major watersheds. For the first objective the existing number of river or streams with coho present in each recovery unit forms the baseline criteria and was obtained from inventory data. Delisting criteria for objective 2 have not been developed for most recovery units and the plan notes that as the timeline for recovery is expected to be 7 generations, or 21 years, abundance criteria will be developed over time. For the third objective, the criteria of having coho salmon in 75% of historically used streams has been established for delisting.

Pacific Northwest salmon: Recovery planning for a suite of ESA-listed salmon ESU's is currently underway by the US Federal Government and other agencies. No recovery plans have been completed, and quantitative goal or objectives are just beginning to be developed.

Recovery is focussed on establishing "Viable salmon populations" (VSP, MacElhany et al. 2000) within each ESU. Viability is defined by four characteristics: Abundance, productivity, spatial structure and diversity.

The process begins by identifying historically demographically independent populations within each ESU. These populations are generally smaller than those

developed using genetically-based criteria for Interior Fraser coho salmon. ESU viability (a criterion for delisting) is achieved when a required subset of the demographically-independent populations are viable, as defined by the 4 characteristics listed above. This subset will include "core" populations and those that provide diversity in distribution and life histories, redundancy as insurance from catastrophic events, and connectness to maintain metapopulation dynamics. Rule sets for describing viability do not identify specific populations, but allow for flexibility in the means to reach the viability criteria. Quantitative criteria for viability standards are lacking, but various categorical scoring procedures have been proposed.

Individual populations are then assessed against the 4 viability criteria. The primacy of population growth rate as a criterion for viability is recognized, and the relationships between population size, growth rate and persistence are estimated using a variety of modeling techniques similar to PVA. Habitat data are then examined to determine whether sufficient habitat still exists to meet requirements for viability determined by the PVA . Finally, in some cases a habitat-based model is available to estimate the capacity of the population's watershed to produce salmon.

These analyses lead to the development of 'planning ranges' for spawner abundances for individual populations. In the case of Puget Sound chinook salmon the recovery goal is for self-sustaining populations at harvestable levels (www.sharedstrategy.com). Consequently the planning ranges are many times higher than the current populations and are closer to the habitat carrying capacity than a minimum population required to avert short-term genetic or demographic impacts. These planning ranges are intended to provide guidance for recovery action planning.

Puget Sound bull trout (May 2004): A total of 57 'local populations' have been identified in this region and 8 'core areas' of high population or habitat value. The recovery targets (objectives) for this management unit are to:

1. Maintain or expand the current distribution in the 8 core areas (this objective contains properly functioning habitat provisions).
2. Achieve a minimum estimated abundance of 10,800 spawners among all core areas. In each of the core areas the adult abundance must typically exceed 1,000 fish. (note: some variations on the 1,000 rule were made because if site specific information. The benchmark of 1,000 individuals was made on the basis of genetic concerns and an analysis of effective population sizes).
3. Restore bull trout to exhibit stable or increasing trends in abundance at or above the recovered target level within the core areas based on 10 to 15 years of monitoring (2 generations).
4. Restore connectivity among habitats.

Summary: Most of the recovery plans contain elements that are found in the 3 salmon plans under review here. The objectives can often be classified into 2 types: those that seek to address the causes of the decline, such as habitat issues, disease, harvest or institutional barriers, and those that are specific population performance targets. The

population targets were usually similar to the criteria identified by the Viable Salmon Population concept, being abundance, productivity, distribution and to a lesser degree diversity. Specific numerical targets for abundance were not common, as all plans noted the considerable uncertainty that existed in establishing them. Where targets were identified they were considered provisional, and subject to modification following further analysis (i.e., bull trout, California coho salmon).

Thus the recovery objectives of the 3 salmon plans are similar in nature to recent plans from other jurisdictions and **therefore can be considered to conform with current practice**. One important difference is that the 3 salmon plans have proposed specific abundance targets for recovery; this is not yet the case for many of the other plans.

Question 1. What is the scientific basis for the minimum population sizes required to achieve the genetic integrity of the salmon populations?

Genetic consequences of small population size

There is now compelling theoretical and empirical evidence that genetic change due to small population size is intimately involved with the fate of endangered populations, both in the short and long term (Frankham et al. 2002). It is important to recognize that the evolutionary process in small populations is fundamentally different from that in large populations. As population size declines, inbreeding becomes unavoidable, and the role of chance predominates over natural selection. Extinction risk is increased by the genetic consequences of small population size, primarily through inbreeding depression, the loss of genetic and phenotypic variation, and the loss of evolutionary potential associated with a reduction in genetic diversity (Allendorf and Ryman 2002).

Genetic diversity refers to the number and distribution of different versions ("alleles") of a gene both within and among members of the group being studied (i.e., a population, species, or group of species). This variation is the "raw material" for evolution because natural selection acts on the phenotypic diversity that arises from genetic diversity. Thus, genetic diversity is necessary for populations to be able to evolve and adapt to changes in their environment. Large populations typically contain higher genetic diversity than small populations of the same species. In fact, the long-term ability of populations to evolve is proportional to the effective population size, both for evolutionary change due to current genetic variation in the population and for changes due to new mutations (Frankham et al. 2002).

Once lost, genetic diversity can only be restored by mutation or by immigration from another population. For isolated ("closed") populations, every effort must be made to prevent the loss of existing diversity because mutation rates are so low that it would take hundreds or thousands of generations to restore levels of diversity typically observed in wild (non-endangered) populations (Frankham et al. 2002). New mutations may be beneficial, favoured in some environments but not in others, selectively neutral, or deleterious. Mutations that affect the phenotype are mostly deleterious and are continually removed by natural selection; the balance between mutation and selection generally maintains deleterious alleles at very low levels. However, the effectiveness of natural selection is reduced in small populations, so that mildly deleterious alleles can accumulate by chance (Lynch and Lande 1998). Recessive deleterious alleles remain hidden in heterozygous individuals because only the dominant, non-deleterious, allele is expressed; the deleterious effects are exposed in homozygous individuals that arise through inbreeding.

Genetic diversity is lost at a faster rate in small populations than in large populations by chance alone – the random process called "genetic drift". An allele will not be passed to the next generation unless at least one individual carrying the allele survives to reproduce. Any allele that occurs at low frequency, is more likely to be lost by

chance from a small population (where it is carried by very few individuals) than from a large population. The consequences of drift can be offset by the immigration (or introduction) of relatively few individuals per generation from another genetically diverse population.

Inbreeding, the mating of related individuals, poses the greatest genetic risk to small populations in the short term, because it reduces reproductive fitness, a phenomenon called "inbreeding depression" (Allendorf and Ryman 2002). Inbreeding is unavoidable in very small populations. It reduces reproductive fitness by exposing deleterious recessive alleles and by reducing heterozygosity where heterozygous genotypes confer greater fitness than homozygous genotypes (overdominance).

Inbreeding has been shown to increase extinction risk in captive populations (Frankham 1995a) but its significance to population declines and extinctions in the wild has been controversial. The response of populations to inbreeding is difficult to predict as there is considerable variation among populations, sexes, and the traits or life history stages most affected (Taylor 2003). Increasingly however, studies are documenting the detrimental effects of inbreeding in the wild (Cronkrak and Roff 1999), and a few studies have linked inbreeding to extinction (e.g., Saccheri et al. 1998). Inbreeding effects have also been found to be more significant in stressful environments (e.g., Coltman et al. 1999). Consequently, inbreeding is now considered a significant threat to population viability, and the development of genetic goals for conservation is becoming more commonplace (Allendorf and Ryman 2002).

How large a population is required to conserve genetic diversity?

All of the adverse genetic consequences of small population size can be related to a single abstract parameter called the 'effective population size' per generation (N_e) . Inbreeding, for example, is expected to increase proportional to $1/2N_e$. A population of actual or census size N_c is said to have an effective size N_e because it behaves in an evolutionary sense the same as an idealized populaton with census size N_e. In an idealized population there is no immigration, generations are distinct and non-overlapping, population size is constant, all individuals are potential breeders and hermaphrodites, union of gametes is random, there is no mutation or selection at any life history stage, and each adult has on average, 1 offspring (with variance =1). These assumptions are clearly not met in salmon, or most organisms, because sex ratios are often biased, male breeding success may be highly variable because of dominance behaviour, the contribution of families to the next generation is usually strongly skewed, and the census population size is far from constant. The main point is that while genetic conservation goals are usually expressed as N_e, the actual number of individuals (spawning adults) needed to achieve the goal will be substantially larger.

Recommendations for genetically-based minimum population levels have been a source of considerable debate over the last 2 decades. The recommended level must satisfy three genetic goals: to retain reproductive fitness by avoiding the short-term and cumulative effects of inbreeding, to avoid the accumulation of new deleterious mutations,

and to retain the ability to evolve in response to changes in the environment (evolutionary potential). Specific objectives such as limiting the loss of heterozygosity to 5-10% over 100-200 years have been proposed under the reasonable assumption that evolutionary potential is related to heterozygosity. An early guideline for N_e was the 50/500 rule (Franklin 1980) based on the theoretical argument that an idealized population of 50 will lose about 2-3% of its heterozygosity per generation, adequate to avoid inbreeding in the short term, and an idealized population of 500 would retain heterozgosity in balance with mutation in the long term. The latter value of 500 has been challenged as being too low on a variety of technical issues, in favour of other prescriptions for 500 to 1250 (Franklin and Frankham 1998), and 5000 (Lande 1995), from which Allendorf and Ryman conclude that an N_e of *at least* 1,000 is required for long term maintenance of genetic variability. Values exceeding 1,000 are likely required for alleles associated with disease resistance (Lynch and Lande 1998). These findings have undoubtedly contributed to the use of 1,000 mature individuals for the designation of *vulnerable* (IUCN) or *threatened* (COSEWIC) under Criterion D, the very small population size criterion.

The relation between N_e and N_c is critical in translating the theoretical guidelines based on N_e to actual population sizes. In general, for all species studied, the most important factor reducing the ratio N_e / N_c is fluctuation in population size, followed by variation in family size, and then variation in sex-ratio. Estimates of effective population size that encompass all the relevant factors average only 11% of census sizes (Frankham 1995b). The Pacific salmon life history (semelparity with overlapping generations) is atypical and has received special consideration (reviewed by Waples 2004a). Waples (2002b) suggests that the within-year ratio (N_{ei}/N_{ci}, the i subscript denoting within-year values) may be about 0.3 for salmon populations, because of factors associated with their mating system, as listed above. However, Pacific salmon mature at multiple ages, providing an exchange of genes among dominant cohorts ('cycle lines') which helps to reduce inbreeding and genetic drift. Simulations by Waples suggests that N_e for a generation can be approximated by the equation:

$$N_e = k^* \, g \, * \, \tilde{N}, \qquad (1)$$

where k is the within-year ratio N_{ei}/N_{ci}, g is the generation length (approximated as 3 years for coho salmon, 4 years for sockeye salmon) and $\tilde{N}$ is the harmonic mean abundance across the 3 or 4 years constituting a generation. The inverse of the harmonic mean is:

$\frac{1}{\tilde{N}} = \frac{1}{g} \sum \frac{1}{N_{ci}}$ where N_{ci} is the census count of spawners for each of the 3 or 4 years. The harmonic mean places largest weight on smaller years where genetic effects are most likely to be important. N_e from equation (1) is a weighted sum of the 3 or 4 years of spawning that contributes to a generation, and will be larger than the N_e of any single year. However, use of the harmonic mean implies that there is a very large penalty for very small spawning populations within a generation.

Equation (1) was tested using a model population with 3 age classes, and was found robust to variations in the maturity schedule (Waples 1990). However, results were

not presented for the case in which >90% of the population matures at a single age, as is often the case for sockeye and coho salmon. In the extreme case where there is only a single age at maturity, the population can be considered to consist of 3 or 4 isolated lineages. Then the effective population size (per generation) for each lineage can be calculated as:

$$N_e = k\, N_{ci} \qquad (2).$$

Now the effective population for each line will be smaller because there is no interchange among cycle lines. It is unclear whether the coho or sockeye salmon cases should be approximated with equations (1) or (2). In the case of Cultus Lake sockeye salmon, non-age 4 fish have at times numbered in the thousands, which should be sufficient to prevent genetic isolation of the cycle lines, and favours the use of equation (1).

In a recent review of models and data Waples (2004) suggests that the per generation ratio of N_e/N_c for chinook salmon should lie in the range of 0.05 to 0.3, where N_e is calculated with (1) above and N_c is the sum of census spawners over the generation. Similarly, Heath et al. (2002) concluded that N_e/N_c for steelhead trout was in the range 0.06 to 0.29. Both of these ranges include the overall average (0.11) reported by Frankham (1995b)

Equation (1) was used to estimate trends in effective population size for Cultus sockeye to illustrate the consequences of reduced *and* more variable escapements in recent years (Figure 1). The plot shows that a dramatic decline in N_e occurred 30 years ago, and that the effective population size has ranged between 182 and 584 individuals per generation over the last 2 generations (8 years).

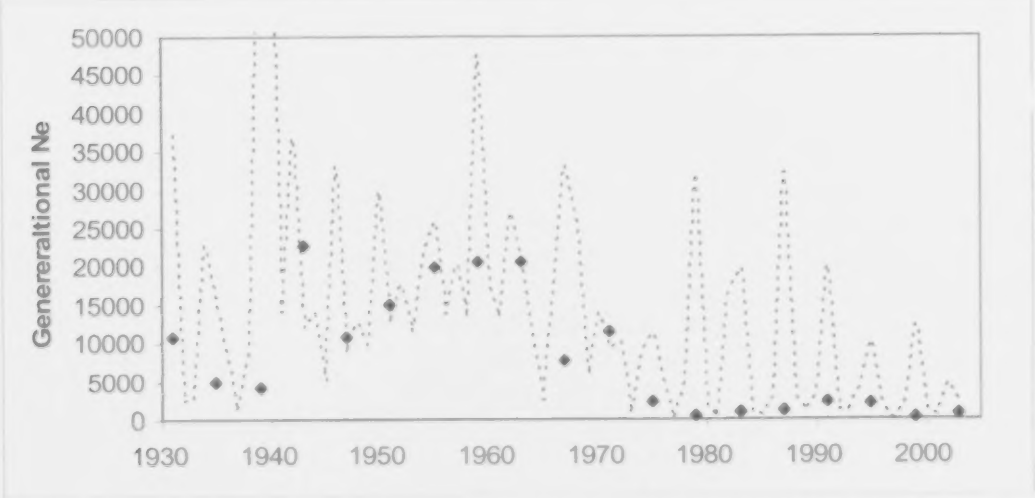

Figure 1. Time series of N_e (from equation 1; diamonds) for Cultus Lake sockeye salmon calculated for 4 year intervals from 2003 backwards. Breeding populations are used in the calculations; losses due to pre-spawning mortality (PSM) were deducted from estimates of adults arriving at the lake. The long term average rate of PSM of 6.6% was used for years without specific data. Dotted line is N_c, the annual number of spawners.

Genetic consequences of supportive breeding with hatcheries

Supportive breeding (typically called "enhancement" within DFO) is a method of boosting population size that involves breeding part of a population in captivity and then releasing the captive progeny back into the wild (Ryman and Laikre 1991). To be effective, survival must be higher in captivity than in the wild, and captive progeny must survive reintroduction to the wild at an acceptable rate. Any increase in population size achieved through supportive breeding will help to prevent extinction by reducing the risk of demographic stochasticity and can, in principle, reduce the rate of loss of genetic diversity through genetic drift. However, depending on the circumstances, supportive breeding may actually reduce the genetically effective population size (Ryman and Laikre 1991, Waples and Do 1994, Ryman et al. 1995). In effect, supportive breeding subdivides the population (in a manner analogous to cycle lines) so that the overall effective population size of the subdivided population depends on the rates of gene flow between the components and the effective population size of each component. The effective population size of the captive component can be maximized (increased to twice that of an idealized population) by careful attention to broodstock collection and equalization of family contributions. However, the effective population size for the overall population is determined primarily by the effective size of the smallest component (Lynch and O'Hely 2001).

It is also important to recognize that the relaxed or antagonistic selection in captivity that occurs with continued supportive breeding will lead to genetic changes (increased "genetic load") that may have pronounced negative effects on the sustainability of the wild population within a few dozen generations or less (Reisenbichler and Rubin 1999, Lynch and O'Hely 2001, Ford 2002). Natural selection can reverse this process once supplementation is discontinued, but it could take several dozen generations to recover a substantial proportion of wild-type fitness, particularly if the captive population has contributed substantially to the natural breeding population in the past (Lynch and O'Hely 2001). Complete replenishment of the captive population each generation (by using wild spawners) will minimize the genetic impact on the wild population, but the impacts can still be large if selection is greatly relaxed in captivity. The genetic changes associated with artificial propagation have long raised concerns about the use of supportive breeding to enhance the ability of a natural population to sustain harvesting (Larkin 1980, Cuenco et al. 1993) or to enhance genetic diversity (Kapuscinski and Lannan 1984, Wohlfarth 1993). In fact, Lynch and O'Hely (2001) conclude that "long-term supplementation programs appear to be incompatible with the permanent maintenance of self-sustaining wild populations".

In summary, it is not possible, within the scope of this paper, to evaluate the potential consequences to genetic diversity of the hatchery operations currently affecting the three salmon populations. That analysis would require a case-by-case examination of the each of the programs currently in place.

An evaluation of the recovery objectives

Cultus Lake sockeye salmon

The objectives of this plan are hierarchical, but Objective 1 specifically addresses the issue of genetic integrity by proposing that the population should exceed a four-year arithmetic average of 1,000 successful spawners with no fewer than 500 in any single year in order to "ensure the genetic integrity of the population".

To evaluate this objective equation (1) was applied to three scenarios of abundances that meet this objective. This calculation is based on the assumption that there is sufficient gene flow among cycle lines caused by the maturity schedule so that all four lines are contributing to overall genetic variability.

Abundances	Generational N_e
1000,1000,1000,1000	1200
500,500,500,2500	625
500,1000,1000,1500	1029

The ratio N_e/N_c ranges from 0.15 to 0.3 (N_c is 4,000 in each case), within the range expected by Waples (2004). Thus results suggest that the abundances stipulated by Cultus Objective 1 are minimally consistent with the current scientific opinion that N_e>1,000 is required to maintain the evolutionary potential of an isolated population. While the objective is near the lower limit for long-term genetic considerations, according to the plan Objective 1 is an interim step towards a broader recovery as identified in Objectives 2-4. Population growth resulting from achievement Objectives 2-4 will reasonably satisfy genetic concerns for this population.

Sakinaw Lake sockeye salmon

Genetic concerns for this population have been raised by COSEWIC as this isolated population declined to levels well below 1,000 spawners in the past 3 generations. Objectives 3, 4, and 5 are hierarchical and seek to rebuild the population from current very low levels to the level identical to the Cultus Lake Objective 1 in 3 generations. Objective 3 specifies the population is to be rebuilt to a minimum of 500 spawners/year in the next generation with a significant reliance on fish culture. Objective 4 is an interim target of 500 naturally produced spawners for the following generation before the final numerical objective of 1,000 naturally produced spawners in the third generation.

The intent of these objectives is to minimize the short-term consequences of the current very small population sizes by increasing abundances as quickly as possible. As in the Cultus case the final abundance objective (#5) likely represents a minimal population size for the long-term maintenance of genetic variation and evolutionary potential. Population levels similar to recent historical data (3,000-5,000 spawners/year) would be more robust in conserving genetic resources compared to the goals specified in the recovery plan.

Interior Fraser coho salmon

The situation for the interior Fraser coho salmon is considerably more complex because the DU spans a large geographic area. Within that area genetic data have been used to identify 5 populations corresponding to major watersheds. Considerably less genetic differentiation occurs among spawners sampled from individual tributaries within the populations, a finding which lead Irvine et al. (2000) and Irvine (2002) to conclude that there was likely considerable genetic exchange among tributaries within populations, but less so among populations.

The recovery plan proposes that a generational mean (using the geometric mean) of 1,000 spawners/year for each population is required for genetic conservation purposes, paralleling the recommendations for the 2 sockeye salmon populations. Application of Equation 1 using a 3-year generation time results in N_e of about 900 if there is little variation in abundance; smaller estimates of N_e will occur if there are years of low abundance. Taken at face value these estimates are on the low end of the acceptable range discussed above.

There are at least 2 issues specific to this case that create additional uncertainty about the evaluation of this genetic recovery objective. First, some of the factors which lead to the within-year inequality between N_{ei} and N_{ei} may be accentuated in the IF populations. These populations occupy very large basins, and when total population is small spawners can become fragmented into small spawning aggregations in the many tributaries. This may create Allee effects, as sex ratio bias and mate finding problems may occur causing some adults to be less successful in contributing progeny. As well, there may be increased potential for inbreeding if homing to natal streams increases the relatedness of matings over what might be expected if the population reproduced in a few large aggregations. These factors would suggest a larger numerical objective could be more appropriate.

On the other hand, each population of IF coho salmon likely receives migrants from one or more of the other populations within the DU which will tend to reduce genetic drift and the loss of heterozygosity caused by inbreeding. Conservation biologists have long used the one-migrant-per-generation rule as a guideline for an appropriate level of connectivity among populations, although a recent review suggests 1 to 10 migrants may be more appropriate (Mills and Allendorf 1996). A crude estimate of the number of migrants among the 5 IF coho salmon populations can be made using Wright's (1931) model (notwithstanding a long list of simplifying assumptions recently summarized by Mills and Allendorf 1996) and F_{st} (a measure of population differentiation) data as:

$$N_e m = 0.25 (F_{st}^{-1} - 1),$$

Where $N_e m$ is the *effective* (sensu N_e) number of migrants per generation. J. Irvine (DFO, Nanaimo) produced preliminary estimates of $N_e m$ using recent genetic data and found an average $N_e m$ for the 5 populations was 6.8 effective migrants per generation. This estimate of gene flow is within the range that has been suggested as sufficient to prevent

the loss of rare alleles within one of the populations through genetic drift (Mills and Allendorf 1996), yet low enough to allow adaptation to local conditions (Wood and Holtby 1998).

Conclusion: The risk of extinction caused by an erosion of genetic diversity in endangered populations has been confirmed by field studies and underscores the importance of guidelines for genetic conservation in recovery planning. We conclude that the recovery targets proposed in the 3 salmon plans *minimally* meet the current scientific standard for population size required to maintain the genetic integrity of isolated populations. But we emphasize that there remains a great deal of uncertainty about genetic conservation guidelines, and accepted values are likely to change over time as our understanding increases.

Question 2: What is the scientific basis for setting abundance targets intended to achieve recovery?

We have interpreted this question to mean: what is the basis for setting abundance targets to minimize extinction risk from non-genetic factors? Our review focuses on the use of population models and other approaches to estimate abundance targets and to review the appropriate objectives of the three recovery plans.

The use of stochastic population models to estimate population persistence began in the 1980's and has expanded ever since. This approach to the assessment of species at risk is usually called Population Viability Analysis (PVA). Early applications of PVA were for the determination of the Minimum Viable Population (MVP), which is the minimum number of individuals required to achieve a specified level of persistence, such as 95% in 100 years. Applications of PVA have subsequently expanded to include the comparison of relative risks of different populations, estimating the efficacy of recovery options, prioritizing research needs, the estimation of habitat needs or reserves, and spatial organization of sub-populations and others (Morris and Doak 2003).

In the past decade the use of PVA models to estimate MVP's for specific populations has fallen out of favour with some conservation biologists. Like all population models, PVA's include numerous simplifications of the biology, and tend to underestimate uncertainty in model structure and input parameters, and MVP predictions are very sensitive to the way the model is constructed (Reed et al. 2002). Caughley (1994) argued that efforts to identify and ameliorate the threats to endangered species and their habitats were likely to be more effective in conservation than the effort expended in modelling and analysing MVPs. Michael Soulé (2002) also notes "*...PVA is easily subverted to finding minimal criteria for short-term viability, as in recovery goals for endangered species. This abuse has distracted population ecologists from the more important problem of ecologically effective numbers and distributions.*". On the other hand, the authors of a recent review of PVA analyses suggest that MVP analyses will continue to be useful in conservation planning (Reed at al. 2003).

It is instructive to use simple generic PVA models to inform decisions about recovery goals for endangered populations. Perhaps the simplest model that is frequently used is the discrete-time geometric population growth model:

$$N_{t+1} = \lambda_t N_t$$

where N is the number of individuals at time t and λ is the population growth rate from t to $t+1$. Here we assume that t is the generation time so that N_{t+1}/N_t is equivalent to recruits/spawner in the salmon lexicon. This is a density-independent model, and when $\lambda>1$ the population will grow unchecked. Random environmental variation is incorporated by specifying that λ is log-normally distributed with parameters in log-space μ and σ^2.

From a given starting population, N_0, and environmental variation, simulated population trajectories will diverge in time depending on the sequence of λ_t for each run.

If a quasi-extinction threshold (QET) is defined as c, the probability distribution of the time to quasi-extinction can be approximated using a diffusion model (Lande et al. 2003) as:

$$g(t \mid \mu, \sigma^2, d) = \frac{d}{\sqrt{2\pi\sigma^2 t^3}} \exp\left[\frac{-(d+\mu t)^2}{2\sigma^2 t}\right]$$

where $d = \ln(N_0/c)$. Here the left-hand term means the probability of quasi-extinction at time t given the 3 input parameters. Value of g can be summed over time to give the approximate cumulative probability of quasi-extinction up to time t. An exact equation is found in Morris and Doak (2003, p. 62).

Analysis of this model was conducted with parameters relevant to salmon populations. The variance was set as $\sigma^2 = 0.2$, which the generational (4-year average) change in spawner abundance for Cultus sockeye salmon, and the model was run with different values for the population growth rate λ.

The probability of quasi-extinction decreases exponentially as the starting population (N_0) increases (Figure 2). This is expected given the formulation for d above. Persistence is generally high (>90%) when N_0=1,000 if λ>1.1 (i.e., a 10% average increase per generation). When there is no long-term expectation for population growth (λ = 1.0), the model predicts that N_0 must be much larger (>5,000) for the population to be persistent over 100 years. Increasing the variance in population growth rate lowers the probability of persistence, and either higher population growth rates or much larger population sizes are required to meet persistence criteria.

Results from the exponential growth model are most relevent to the case of a population well below carrying capacity, and even then are optimistic with respect to population persistence. Higher risks of extinction are expected in any model that includes a carrying capacity because the carrying capacity can be considered a 'reflecting boundary' that could send some trajectories back towards the QET. Unfortunately there is no simple analytical model for this case (Morris and Doak 2003).

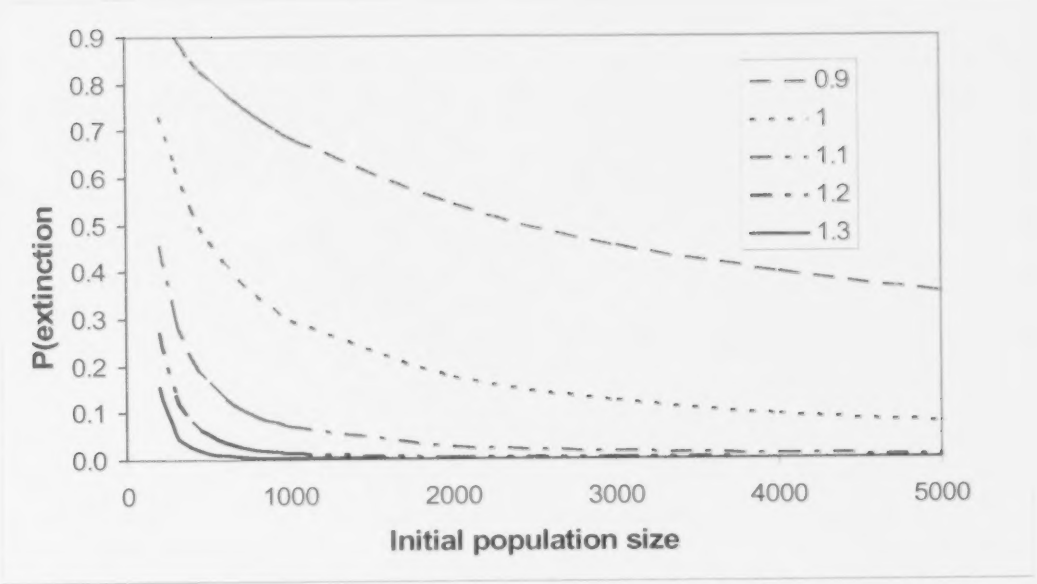

Figure 2. Density-independent diffusion model results for a population with $\sigma^2 = 0.2$, QET =100 and various values of λ, as indicated in the legend. Calculations are for 25 generations, (i.e, 100 years in the case of sockeye salmon).

A second model useful for reaching generalizations about population persistence is the Population Change Criteria (PCC) model developed by NMFS for Pacific salmon (available at http://research.nwfsc.noaa.gov/trt/viability_pcc.htm). This model uses the same geometric growth model, but it is a simulation model that includes four cycle lines, and uses the 4-year running average abundance to evaluate status against the QET. A single age at maturity is assumed. Recognising the importance of population growth rate in affecting persistence, the model is structured to identify the combinations of λ and N_0 that meet the specified persistence criteria. The model calculates the expected population size over a short-term-planning horizon, such as 20 years, given a value of λ and sets this population size to be the carrying capacity for the population. Thus the expected population size at the end of the planning horizon is considered to be a precautionary estimate of capacity (P. MacElhany, NMFS Seattle, Pers. Comm.).

The PCC model was run with 2 different values for the variance in growth rate and a 20 year planning horizon, and it produced similar, but not identical results to the diffusion model. Generally higher growth rates are required for persistence in the PCC model because the average population size after 20 years is often small, which causes the the carrying capacity to be small for the rest of the simulation. Figure 3 shows the combinations of population growth rate and initial annual population size that result in 95% persistence in 100 years (25 generations). Note that high growth rate is most critical for very small initial populations, and the required growth rate decreases exponentially with increasing initial population size. Higher variability in growth rate results in a more stringent requirement for population growth rate.

The model was also run with a much longer planning horizon to allow the model to have a carrying capacity closer to the Cultus Lake case. Beginning with 1,000

individuals, and a time horizon of 75 years, the eventual population size is about 53,000 with a generational growth rate of at least 1.25 required for persistence. The high growth rate is most needed in the first few generations when the population is smallest and most at risk. This result is closer to that of the diffusion model, presumably because the effects of the carrying capacity are much weaker when the planning horizon is longer and the carrying capacity higher.

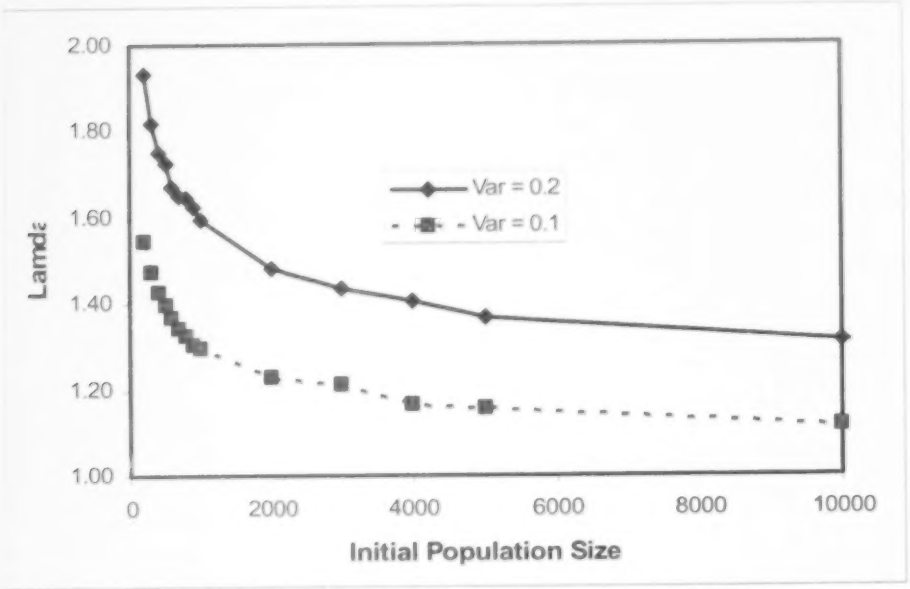

Figure 3. PCC model results. Combinations of initial population size and average population growth rate that lead to a probability of persistence over 100 years of 0.95 consisting of 20 years of population growth to a carrying capacity are shown. Persistence is defined as having a 4-year average abundance>QET of 100 individuals.

The generalizations that can be drawn from both models are: (1) persistence is possible for small initial populations but only if λ is high; this dependence drops as $N_0 >>$ QET, (2) A positive average generational growth rate, perhaps in the range of 10-40% increase per generation is required to reduce risks to small populations and (3) much larger initial populations are required if $\lambda \approx 1$.

There are a number of PVA analyses specific to salmon populations that have appeared in the literature. Perhaps the first is the analysis of Snake River chinook salmon (Emlen 1995), which was based on a Ricker model. The probability of extinction was found to be very low under the estimated parameters because productivity was sufficiently high (Ricker α= 1.9-2.8; α is analagous to λ) for population growth. Emlen (1995) noted that extinction was much more likely if α fell to less than half the current value.

A model of Umpqua River chinook salmon assembled by Ratner et al (1997) resulted in an estimated λ = 1.09, and the authors concluded there was a negligible risk of extinction over 100 years, even though the population consisted of only a few hundred

spawners. However, they defined extinction as an absence of fish in any single year, so their estimates of risk are lower than analyses that use a QET.

Nickelson and Lawson (1998) used a detailed habitat-based model to evaluate the risk of extinction (defined as <50 spawners) for Oregon coho salmon. They found the risk of extinction was generally low, even for initial populations of only a few hundred fish. It is not possible to extract estimates of λ from their model, but results presented on population growth rates as a function of marine survival rates and fishing mortality suggest that conditions were adequate for positive population growth most of the time. Metapopulation dynamics contributed to population persistence in this analysis.

The viability of winter-run chinook salmon of the Sacremento River was modelled by Botsford and Brittnacher (1998), who found that the risk of extinction generally decreased when there was greater variation in the age of maturity (through risk spreading). Their model also generated inverse relations between population growth rate (cohort replacement rate) and initial population size that were similar in form to those of the simple models presented above. This led them to recommend that delisting criteria include both a target population size and a population growth rate, as well as an allowance for the uncertainty in estimates of population parameters. Because the population had a negative growth rate, they recommended a recovery objective of >10,000 female spawners.

Finally, results from stochastic simulation model for Cultus Lake sockeye salmon were presented in COSEWIC (2003). Productivity at low population sizes was estimated from a Ricker model, and was in the range of 3 recruits/spawner in the absence of fishing or pre-spawning mortality (PSM). Results from the model indicated the risk of extinction (Abundance less than a QET of 100 in 4 successive years, 25 generation time horizon, starting with the 1999-2002 escapements [mean 4750]) was generally very low unless the combination of prespawning mortality and/or fishing mortality exceeded about 65%. Given the estimated inherent productivity of the stock, these additional sources of mortality would serve to bring the replacement rate down to unity or less, increasing the likelihood that the high variability in recruitment observed for this population could result in extinction.

A common feature in most of the MVP determinations from the more detailed salmon models is that the study population was reduced below the carrying capacity of its habitat by factors affecting productivity (independent of population size) such as fishing, disease, ocean conditions or hydropower impacts. If these impacts could be reduced, in theory, the high intrinsic productivity of these populations should result in rapid rebuilding to the carrying capacity, thereby minimizing the risk of extinction. Under this scenario, the starting populations can be quite small, just as suggested by the diffusion and PCC models (Fig. 2). Unfortunately, in reality, recovery is not guaranteed because of chance events, unanticipated changes in the ecosystem or other factors that have the potential to limit population growth.

In addition, there is an important yet subtle difference between PVA's conducted for Pacific salmon and many of those conducted for non-exploited wildlife species.

MVP's for non-exploited wildlife are typically calculated to determine the amount of habitat required for the population to persist, to plan land-use, habitat restoration or reserve development. Because the initial population size in these models is considered to be at the carrying capacity (Lande 1993, Reed et al. 2003), the simulated populations cannot increase beyond initial values, although they may decline because of stochastic events. Populations with high intrinsic growth rates can recover more quickly from a downward deviation cause by years of poor survival or recruitment. Reed et al (2003) found an inverse relation between MVP and the estimated λ for the population: with λ=1 the average MVP was 13,500 adults (99% persistence over 40 generations), and for λ=1.6 (the average of 106 vertebrate PVAs) the MVP was reduced to 6,000 adults. Again, these abundances are much higher than for Pacific salmon because the MVP is also the carrying capacity; diminished salmon populations are expected to grow considerably beyond the MVPs to a potentially much higher carrying capacity.

An evaluation of the recovery objectives

Cultus Lake Sockeye Salmon: Objective 1 is designed to protect the genetic integrity of Cultus sockeye by requiring a generational average of 1,000 spawners (no single year < 500); this objective is also a baseline for demographic considerations. Objective 2 seeks population growth at a generational scale by requiring cycle over cycle growth (N_{t+4}/N_t > 1) in three of 4 cycles. No specific growth rate targets are identified, but the analysis of the historical data showed that an average generational growth rate of > 1.5 occurred when 3 of 4 cycles incurred increases (Fig. 4).

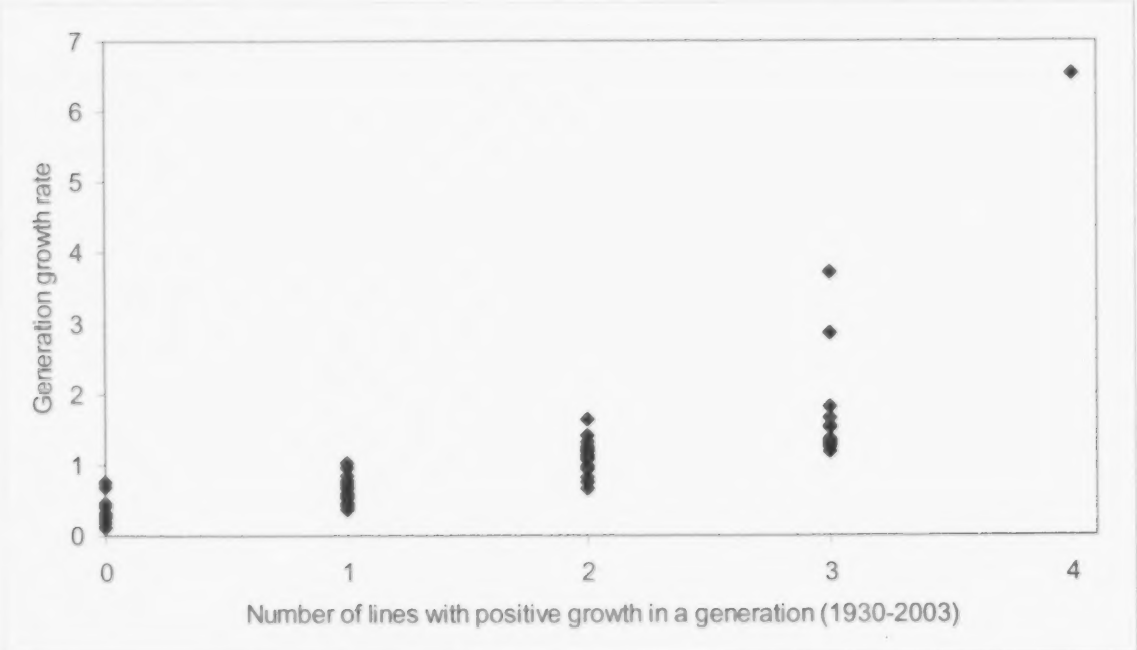

Figure 4. Using the 1930-2003 spawner data the generation growth rate is plotted against the number of lines in that generation that showed positive growth. This was done by comparing the geometric mean

abundance over 4 consecutive years with the geometric mean of the next 4 years. This procedure was repeated with annual increments to 2003. The results show that growth rarely occurred in 4 consecutive years (only one instance in 74 4-year windows). However, the generational growth averaged >50% per generation and was always positive ($\lambda > 1$), as long as 3 of 4 lines showed growth. In contrast, when less than 3 of 4 lines showed growth, generational growth was more variable and frequently negative ($\lambda < 1$). Note that this analysis is based on spawners only and therefore includes the effects of historical fishing patterns on brood productivity.

Analysis: As discussed in the review of general PVA analyses above, a base population of 1,000 individuals and an expectation of strong positive growth rate should be adequate to minimize the probability of extinction in the short term. There is no guarantee that if 3 of 4 lines show an increase the generational growth rate will be as large as was found in the historical data. At low abundance (< 5,000 spawners), depensatory mortality in the lake may constrain population growth for some cycle lines (see section 3) and this could reduce generational growth and increase extinction risk.

Sakinaw Lake Sockeye salmon: Objective 2 in the Sakinaw Sockeye Recovery Strategy also seeks generational growth by having cycle over cycle growth for 3 of 4 cycles, based on the analysis of historical data for Cultus sockeye. Objectives 3 to 5 identify abundance targets that result in the population increasing from the current generational average of about 50 fish to an average of 1,000 fish by 2017, 3 generations from the present. This is a very high rate of generational growth (170%/generation) requiring aggressive management measures and hatchery interventions.

Analysis: Because the Sakinaw sockeye population is currently very small, objectives to achieve a very high rate of generational growth using aggressive measures are consistent with the generic PVA analyses that show the strong dependence of population persistence on growth rate. However, it must be noted that even after a population size of 1,000 individuals is achieved, standards for population persistence may not be achieved unless the population's intrinsic (natural) productivity remains high enough to permit natural recovery from periods of adverse survival. Similar concerns apply to the choice of long-term goal (Objective 7, yet to be determined) presuming that it may be similar to the historical average escapement (5,000 spawners). The inclusion of a population productivity objective in the plan would provide greater assurance that the population would be viable over the long term.

Interior Fraser Coho salmon: The analysis of demographically-based recovery goals for IF coho salmon is found in Section 4.

Summary- The determination of abundance levels that would result in populations being considered 'not at risk' depends on the conditions and context in which the analyses are being conducted. For any specified population size (all other factors being equal), populations with low intrinsic productivity are at greater risk of extinction than more productive populations, because the latter can rebuild more quickly when population size is reduced through adverse events. Conversely, to provide the same chance for persistence, the minimum abundance objective must be higher for a population that is intrinsically unproductive than for one that is intrinsically more productive. Thus, a small

productive population whose population size is constrained by carrying capacity may be at less risk of extinction than a larger but less productive population.

For exploited populations the risk to the population at specific abundance level will depend on how harvest is managed. Harvest can be considered an additional factor that will both reduce λ and increase its variability, both of which will decrease population persistence (Fig. 3). *If the abundance benchmarks in the recovery plans are used as targets for fisheries management resulting in expected population growth rates being reduced to $\lambda=1$ (i.e,. replacement) the risk to the populations will be significantly higher than the case in which the targets are coupled with an expectation of $\lambda > 1$.* This concern is reduced if cohort productivity can be accurately predicted and harvest rates manipulated so that there is positive covariation between productivity and harvest. In the case of Interior Fraser coho salmon time series analysis and environmental predictors may have utility in forecasting ocean survival rates, a major contributor to variation in productivity. These forecasts might allow harvest rates to be set to ensure population growth across a range of ocean survival conditions.

Thus we conclude that the current abundance-based guidelines of about 1,000 spawners per year should be viewed either as interim short-term targets, or they must be coupled with a plan for the management of population productivity to ensure that the average $\lambda > 1$.

Question 3: What is the scientific basis for minimum population sizes in the face of demographic issues such as depensation or predator pits as identified in Cultus Objective 3?

Depensation refers to the situation in which the productivity of a population is reduced at low abundance. A variety of mechanisms that cause depensation have been identified, including reproductive failure and predation. Reproduction may fail at low abundance due to problems in finding mates, fertilisation success, or a breakdown in social structures related to parental care. Predators will cause depensatory mortality whenever their consumption of prey remains relatively high despite a decrease in prey abundance. The impact of predators on a salmon population (expressed as percent mortality) is typically depensatory (e.g., Wood 1987) and can be much higher in years of low salmon abundance than in years of higher abundance when the impact of predation might be small (Liermann and Hilborn 2001). In the extreme, depensatory mortality caused by predators can cause overall productivity (e.g., smolts/spawner) to decline at low salmon abundance, resulting in depensation at the population level. Depensation places small populations at very high risk because the population may not be able to sustain itself and is thus doomed to extinction.

Another scenario is a "predator pit" in which the corresponding stock-recruitment curve is concave-up (pit-like) near the origin such that average recruitment exceeds replacement both at very low and high spawning abundances, but not at intermediate levels. This kind of predator pit could arise from a Type III (sigmoid) functional response to prey density wherein predators "switch" away from a prey species at very low abundance (Holling 1959). Under this scenario there are potentially two stable domains for the prey species, one at very low abundance and the other at a higher level at which the impact of predation is lower. There is also an intermediate unstable region where the population could move in either direction to one of the stable domains.

In PVA, the largely unknown potential for depensatory processes at very low abundances is practically dealt with using the quasi-extinction threshold (QET). This is usually a low threshold below which the population is considered effectively extinct because there is significant uncertainty about both the genetic impacts (i.e., inbreeding) and population dynamics, including depensatory demographic effects that include random variations in sex ratio, and ability to find mates in space and time. The 3 salmon recovery plans use a QET of 100 spawners in all consecutive cycle lines of a complete generation; this threshold is within the range used for other species (Morris and Doak 2003).

Depensation and Cultus Lake sockeye salmon- The analysis of depensation in Cultus sockeye was initiated by the CSRT because productivity measured as the rate of smolt production (i.e., smolts/spawner) in the last few broods has been well below the average in the historical database. Two hypotheses have been proposed to account for this observation:

1. There has been a recent change in the Cultus Lake environment that has caused the spawner-smolt survival rate to decline. Potential mechanisms include:

a. Reproductive failure caused by PSM that was unaccounted for by field programs or other means,
b. Reduced incubation success caused by changes to spawning areas, including groundwater conditions, gravel quality, milfoil or predation.
c. Lower fry-smolt survival caused by reduced lake productivity, increased competition from other species, or increased predation, perhaps caused by pikeminnow populations enhanced by the presence of milfoil.

2. The alternative hypothesis is that depensatory mortality processes have and continue to exist in the lake. The recent low smolt production rates have also been years of low spawner abundance; both current and historical small broods have resulted in weak smolt production.

These issues were explored with the time series of smolt and spawner data for Cultus Lake sockeye. Although the data span a period of 80 yrs they are intermittent and there are a number of issues that could confound the analysis. Specific treatments of the data include:

1. "Spawners" here refers to those counted at the fence.
2. Early broods that were affected by hatchery operations or predator control were removed (most years between 1926-1942).
3. Spawner estimates for the 1988-1991 broods were adjusted upward to account for a particularly short period of operation of the adult counting fence. The multipliers were based on the historical timing as resulted in expansions of 3.1, 1.4 and 1.6 respectively to the fence counts presented in Schubert et al. (2002).
4. The 1989 and 1990 broods were affected by predator control but are included and highlighted in red. During these years a summer pikeminnow removal program captured about 10% of the population in each year.
5. The 1999 and 2000 broods were likely affected by very high prespawning mortality and are shown but not included in the calculation of averages (about 5 smolts/spawner in each year).
6. The 2001 brood was probably affected by PSM, but no direct estimates are available.
7. The 2002 brood suffered a 13% loss due to PSM which is not accounted for in the figure- smolts/effective spawner would be correspondingly higher.
8. For clarity the figure is cut off at 40,000 spawners. The 2 broods with higher escapement are not shown, but are included in the calculation of the averages.
9. Age data are not included in the most recent smolt runs, which will introduce small errors.

Visual examination of these data (Figure 5) suggests two groupings: at spawner abundances greater than approximately 7,000 spawners the smolt production rate is variable but has a geometric mean of 61 smolts/spawner (90% CI 48-77). At abundances <7,000 the production rate is 33 smolts/spawner (CI 26-42) excluding the 2 predator control years or 40 smolts/spawner (CI 29-53) including the predator control years.

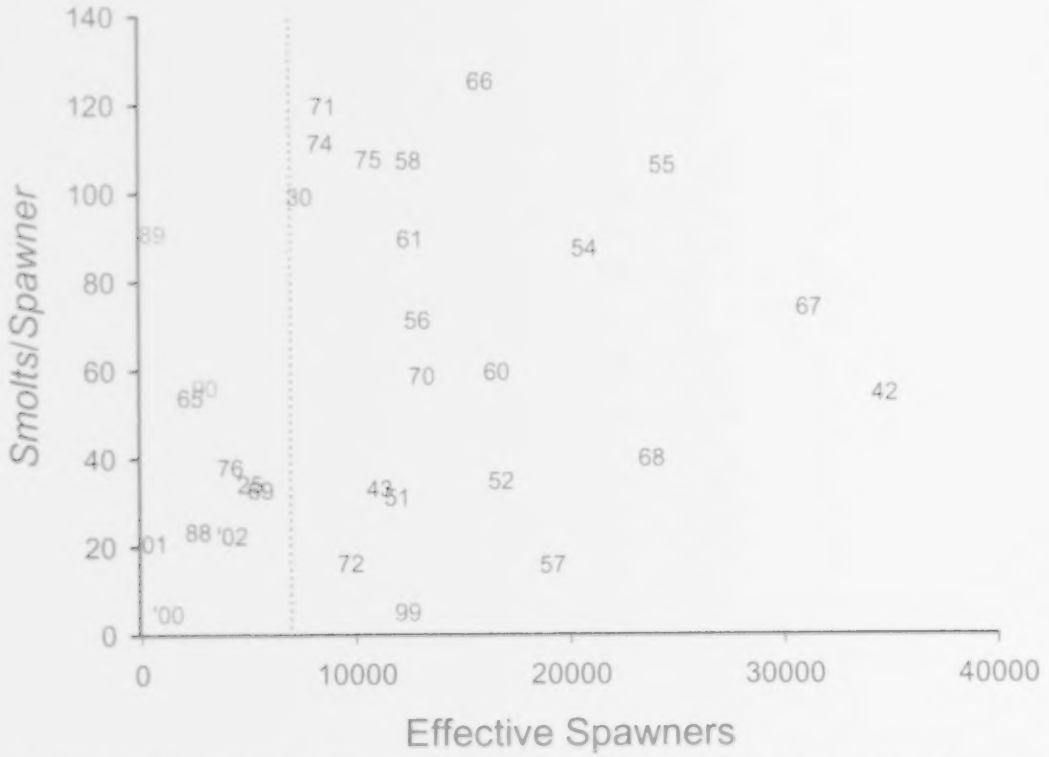

Figure 5. Relation between smolts/spawner and spawners for Cultus Lake sockeye. Points appear as brood years. Brood years 1989 and 1990 (red) were affected by pikeminnow removal program that removed an estimated 10-20% of the population. Brood years 1999 and 2000 were likely affected by high rates of PSM and are not included in the calculation of average production rates.

The low productivity cluster includes many of the recent broods, but also includes 5 small broods dating from the period 1925 to 1988, of which none produced more than 50 smolts/spawner. This pattern provides evidence against the hypothesis that there has been a recent change in the lake that has resulted in poor survival of the recent small broods. Rather, small broods from throughout the period of record have, on average, performed poorly compared to those in which the spawners exceeded >7,000.

One component of the change in lake productivity hypothesis that can be evaluated with historical data is the relation between smolt size and abundance. If productivity of the lake has declined recently, smaller than expected smolts (i.e., negative residuals) are predicted for the recent years. This prediction is not supported by the data (Figure 6). Schubert et al. (2002) note that there is no evidence that the limnetic zone of the lake has changed.

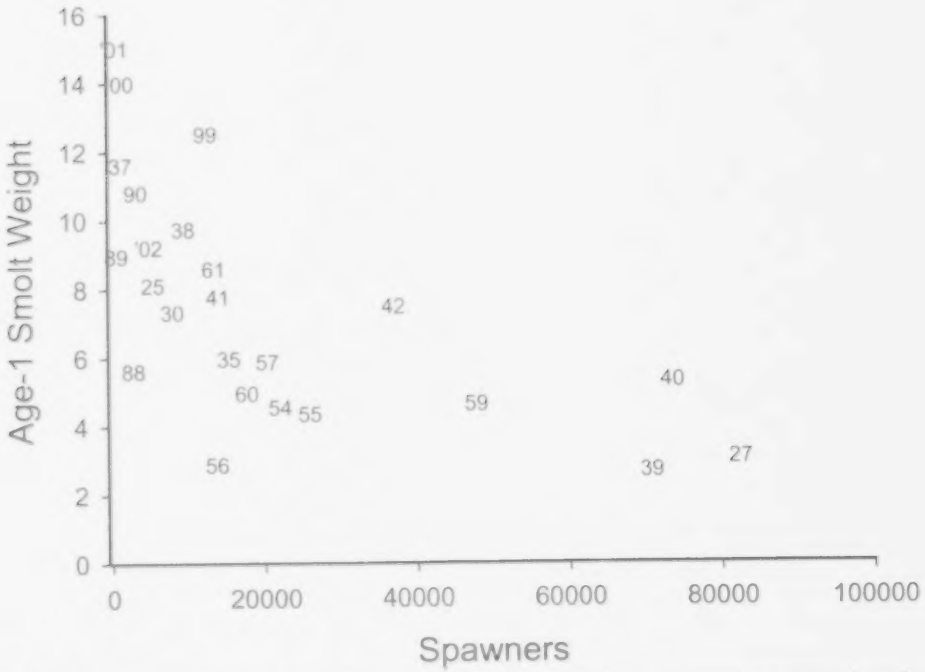

Figure 6. Relation between age-1 smolt weight and the abundance of parent spawners; brood years are indicated on the figure. Note that recent broods are generally above average in size.

The implication of depensatory mortality is that population has less potential for rebuilding, or sustaining exploitation when abundance is below the threshold of about 5-7,000 spawners. For example, the recent smolt production rates of about 20-25 smolts/spawner, when coupled with a marine survival rate of 5% (the geometric mean of Cultus data in Schubert et al. (2002), excepting the 1951 outlier) yields R/S =1 to 1.25. At this low level of productivity the population has much less capacity to grow if additional sources of mortality such as PSM or fishing occur. When smolt production is 60-70 smolts/spawner, average R/S increases to 3 which gives the population headroom to absorb the effects of PSM or sustain fishing mortality.

Additional evidence for the hypothesis of lower productivity at low population sizes was reported in the Cultus Lake recovery strategy by making use of the time series of the four cycle lines of spawner abundance. It was noted that after the hatchery/predator control experiments were completed in 1942 the abundance of a cycle line has rarely recovered once it fell below 5,000 spawners (Figure 7). This threshold was crossed in the 1960s for the 2001 cycle line, the 1970's for the 2000 line, the 1980's for the 2002 line. The 2003 line crossed the 5,000 mark last year (largely due to PSM); it remains to be seen whether it can recover.

Following the analysis of the smolt data above, it was hypothesized that smolt production rates when the spawner abundance was small were too low to allow for population increases under the exploitation and ocean survival rates that were

experienced by the population. Exceptions to the pattern of continued decline after abundances go below 5,000 fish occurred prior to 1940. The 2001 line declined steadily from 1925 (a poor smolt production year) to 1937, but the 1937 brood seemed to benefit from the cumulative effects of 5 years of predator control (resulting in 160 smolts/spawner) which kickstarted the population to higher levels of abundance. Similarly in the 2000 line the 1932 and 1936 broods were apparently assisted by hatchery operations and predator control which lead to high smolt production rates and a dramatic increase in abundance.

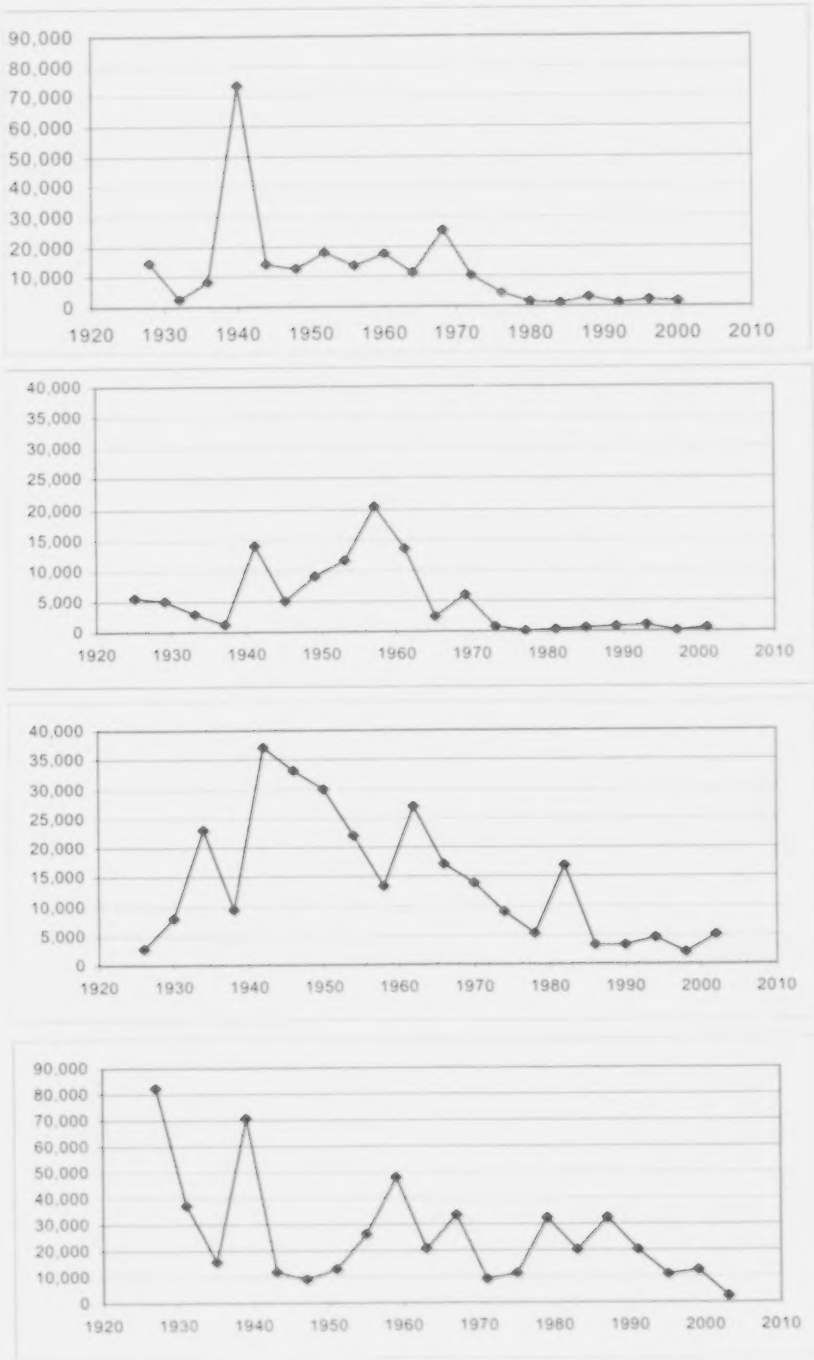

Figure 7. Time series of the 4 cycle lines of Cultus Lake sockeye salmon, labelled in the text as the 1999-2003 cycle lines. Most broods between 1926 and 1942 were affected by either hatchery operations or predator control.

Despite these 2 lines of evidence for the depensatory mortality hypothesis, the patterns may have arisen by chance. Ideally, biological information on the mechanism causing the apparent patterns in mortality would be available for additional support. In the case of Cultus Lake a great deal of work on the predators of sockeye juveniles has been conducted (Ricker 1941), but the available data are not adequate to evaluate the potential for depensatory mortality at low levels of salmon abundance. However, a number of studies focussing on the predation by trout and charr on migrating fry and smolts have found that depensatory mortality can occur when there are large aggregations of predators in outlet streams that have the potential to exert high rates of mortality on smaller smolt runs (see review in Peterman and Gatto 1978, Ruggerone and Rogers 1984). Northern pikeminnow, a known predator, aggregate at the outlet of Cultus Lake during spring, but their impact on migrating smolts relative to the predation that occurs over the rest of the year is unknown.

Conclusions: Based on the information presented above, the CSRT identified the issue of freshwater productivity as a potential limiting factor for recovery from the current population levels. The team considered that the question "*is freshwater productivity adequate to support recovery?*" would have to be answered in the affirmative for recovery. The current smolt production rates, and the analysis of the historical data provide sufficient evidence to highlight this as a concern. Continued monitoring of adult and smolt populations will allow an assessment of whether the low production rates will continue. Field programs at Cultus Lake will provide further insight into the role of pikeminnow as an agent of depensatory mortality, and predator control programs may be able to alleviate some of the mortality on juveniles and smolts. Control programs do imply a long-term commitment, as predator populations have the potential to rebound quickly after control programs are ceased.

However, if smolt production remains low for spawning populations less than 5,000 fish, recovery will depend on minimizing all sources of mortality that can be controlled *and* a period of above-average survival in both freshwater and marine stages of the life cycle. The historical time series of spawner abundances for the 4 cycle lines (Fig. 7) highlights the difficulty in recovering from low abundances.

4. What is the scientific basis for setting generational average escapement for Interior Fraser coho unit as a whole and at the population and subpopulation levels?

The establishment of recovery targets for this DU poses particular chailenges because the DU occupies a large area, and spawners are found in many locations. The stated recovery goal is to secure the long term viability and *diversity* of the DU. The preamble to the recovery objectives notes that recovery will require adequate numbers of individuals, and maintenance of the spatial distribution and genetic and life history diversity found within and among population.

The DU was divided into 5 populations based on genetic information (Irvine 2002). Within each population one to three demographically distinct sub-populations were identified using a variety of subjective indicators. Sub-populations were defined as being demographically independent, meaning that the population dynamics of one sub-population would be unlikely to affect the dynamics or abundance of another. Genetic exchange among sub-populations is expected to occur at greater rates than observed among populations, and would likely exceed 10 effective migrants/generation. Sub-populations were delineated on the basis of large watersheds or lakes, or partial barriers to migration. No particular status was given to spawning aggregations (e.g., the fish in a tributary stream) as demes have been observed to be ephemeral, and considerable interchange among nearby streams seems to occur.

The Recovery Team decided that to meet the diversity component of the recovery goal all five populations should remain viable at all times, and that this would be achieved by meeting abundance objectives in some of the sub-populations within each population. This approach was modelled after the US model for ESU viability (McElhaney et al. 2000), which identified the need for spatial and genetic diversity. It was largely the Recovery Team's vision that recovery required the maintenance of all of the current populations, rather than any specific scientific criteria, that lead to the development of the criteria.

Objective 1 of the plan requires that at least half of the sub-populations found within each population maintain a 3-year geometric mean abundance of 1,000 spawners so that there are demographically robust sub-populations throughout the range of the DU. A generational average of 1,000 is adequate for genetic concerns as it will result in a generational N_e of approximately 500-1,000 (Section 1, Equation 1), unless there is a very large discrepancy in the line sizes. Four of the populations have 2 or 3 sub-populations which exchange enough individuals that genetic conservation goals should set at the population level, resulting in a much larger N_e.

A generational average of 1,000 individuals was also considered adequate from a demographic perspective. Based on the preceding review of MVP analyses a demographic recovery goal of 1,000 individuals in a sub-population with an unspecified growth rate target should be considered marginally suitable for assuring population persistence. However, within each sub-population there is usually a number of spawning aggregations, or demes, sometimes distributed over a large area. Thus most of the sub-

populations can be considered metapopulations, in contrast to the single, isolated, populations analysed in most PVAs. In general, metapopulations tend to have a greater probability of persistence than a single population of similar size because of any spatial variation in environmental conditions will cause asynchrony in population fluctuations among demes, reducing the probability that all demes will become extinct simultaneously because of environmental variation. Dispersal or straying from streams that are more productive or are doing well can then help rescue demes experiencing poor survival. Hill et al. (2002) found that relatively small rates of dispersal or straying among metapopulation components have a large impact on the time to extinction of an individual stream because of the rescue effect. In a metapopulation model for Oregon Coast coho salmon Nickelson and Lawson (1998) found that only demes using high quality stream reaches were able to survive periods of poor ocean conditions, and strays from these areas recolonized poorer quality reaches when conditions improved. Bradford and Irvine (2000) documented that less impacted (i.e., better quality) streams in the Thompson Basin declined less rapidly during the recent period of declining survival suggesting that there is variability in the productivity of individual streams and potential for exchange among areas of differing productivity. Unfortunately it is not possible to estimate the increase in persistence that a coho metapopulation of 1,000 spawners might have over the case of a single deme of similar size.

An analysis of the intrinsic productivity of the Thompson populations also supports the use of the 1,000 generational average as an adequate MVP. This analysis showed that the recruits/spawner ratio of the Thompson populations was correlated with marine survival rates of Georgia Strait wild coho salmon, and that the average R/S (equivalent to λ) was greater than one in all but the years of poorest ocean survival. This means that if harvest rates and other management actions are managed in response to ocean conditions, there will likely be sufficient productivity to ensure the potential for population growth in most years. The management of threats to the population, including harvest, were addressed in Objective 2 of the recovery plan.

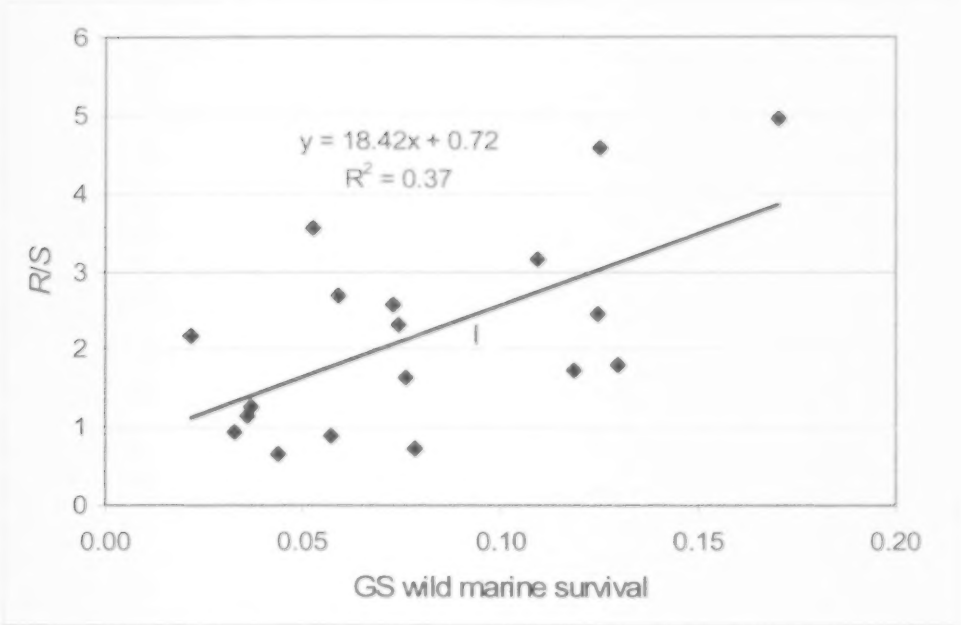

Figure 8. Relation between average recruits per spawner (1984-2000 brood years) for North and South Thompson coho salmon populations and the average marine survival rate for Strait of Georgia wild coho salmon indicator populations (Strait of Georgia data from K. Simpson, DFO, unpublished data).

Sub-population recovery targets and abundance across the whole DU. The recovery team recognized that the sub-populations are different in size and possibly productivity, and that at any point in time not all sub-populations would have the same status relative to the recovery targets. Thus the recovery objective one stipulates that at least half of the sub-populations of each population must meet the recovery target. This requirement ensures that there are viable populations across the geographic range of the DU, which serves to protect the DU from regionally catastrophic events and preserve some of the genetic and life history diversity, as stipulated by the recovery goal.

Hypothetically Objective 1 (Appendix A) requires 1,000 fish in a total of 7 of the 11 sub-populations, yielding a minimum total of 7,000 spawners per year for the DU. This scenario is unlikely because some subpopulations will have more than 1,000 spawners for the 7th to reach 1,000, and there will be some fish in the remaining 4 subpopulations that do not meet the recovery criterion. Therefore it is likely that the DU-level of abundance that meets Objective 1 will be substantially higher than 7,000 spawners.

Historical spawner data were examined to estimate the likely total DU abundance that would satisfy the viability criteria of Objective 1. This analysis showed that populations failed to meet the criteria of having sufficient sub-populations with 1,000 spawners (generational average) when the generational average estimated abundance for the whole DU was less than 20,000 fish. This occurred in 4 years from 1996-1999 when the DU was at its lowest abundance. The utility of this estimate for the future is

contingent on the patterns of relative abundance among sub-populations continuing in the future, and that there is consistency or standardization in the escapement monitoring program so that past and future estimates are comparable.

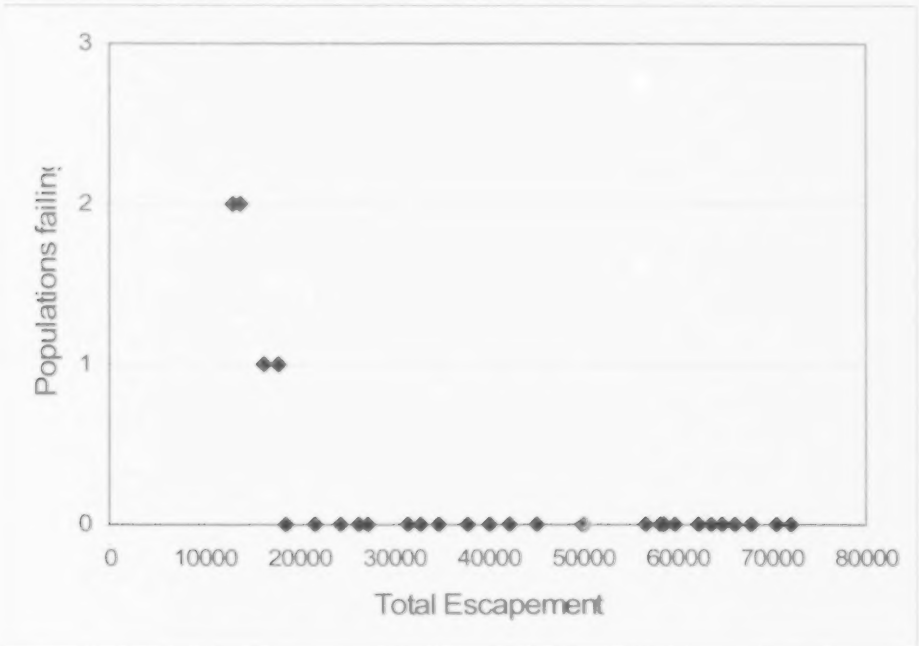

Figure 9. Relation between the number of populations (of 5) that fail the recovery objective criterion of having sufficient subpopulations with >1,000 spawners, and the total estimated abundance of spawners for the whole DU. Here abundance is expressed as the geometric 3-year average.

5. **Final Comments.**

The determination of measurable, objective recovery targets is a challenging task for recovery teams. Part of the challenge stems from the diversity of views among team members about what represents 'recovered'. Those views may be conditioned on social or economic implications of recovery as well as observations of the recent history of the population. In reviews of ESA recovery plans Tear et al. (1993, 1995) noted that recovery goals of many plans were at or below current population levels, and were at levels that would not meet IUCN criteria. They suggested that in many cases goals were not biologically defensible and would be risky for the species in question. Similarly, in a review of ESA-listed bird species Elphick et al. (2001) found that >75% of the variation in recovery goal population size could be explained by the size of the population at the time the plan was written and found that biological information and analyses did not play a detectable role in recovery goal size. They hypothesized that the decision made by recovery teams might be influenced by whether management actions might be tolerable or feasible, and thus might be reluctant to suggest goals significantly larger than the current population.

Uncertainty about setting recovery goals can also result from a lack of knowledge and data for the species (Tear et al. 1995), however, the 3 salmon populations under review are very well studied relative to most species at risk. Nonthlesss there remains large scientific uncertainty in estimating the risk of extinction for threatened populations, partly because conservation biology is a relatively young science, and extinction itself is not an easy phenomenon to study.

The 3 salmon recovery teams have used a common approach for the identification of genetic and demographic risks, and adapted those to the specifics of each population. The use of generic, non-specific, criteria does create the potential for discordance between the recovery goal and the size of the population, either as recently observed or as potential based on the amount of habitat present. A comparison of the recovery objectives with recent historical abundances indicates that the recovery targets are all less than one third of recent maxima (Table 1). Since these maxima were during periods of fully-developed industrial fisheries, it is likely that the recovery goals are in the range of one-sixth or less of the potential capacity of their respective habitats. *Thus the teams have been consistent in interpreting recovery to mean an abundance at the lower range of the spectrum of values they might have considered.*

Population	Historical Abundance[1]	Recovery Objective	Proportion of historical abundance	Proportion of most recent generation[2]
Sakinaw	5,000	1,000	20%	2500%
Cultus	20,000	1,000 or 7,000[3]	5 or 35%	64-448%[4]
IF Coho (total)	70,000	20-25,000	29-36%	57-71%
IF Coho (populations)	4,400-27,000[5]	1,000	4-23%	8-25%
IF Coho (sub-populations)	1150-11,600	1,000	9-87%	19-57%

[1]Approximate generation geometric mean for the period of highest abundance in the escapement data record. For Cultus this does not include the period of predator control in the 1930s and 1940s.
[2]Geometric mean of last 3 or 4 years of spawner abundance
[3] Higher value reflects Cultus objective 3.

[4]Recent data for Cultus do not include PSM. Percentages would be much higher if effective spawners were used in the calculation.
[5]This is the range of generational mean abundance among the 5 populations.

Table 1. Summary of recovery objectives in relation to recent and historical abundances of spawners.

Throughout this report we have argued that the setting of relatively modest recovery targets (Table 1) will not ensure the persistence of these populations without corresponding targets for the management of population productivity so that the long-term expectation for population growth is positive. Thus the recovery goals should not be viewed as fishery management targets. While the desire to maintain or improve productivity is embodied in the plans, more work could be done to create objective, measurable targets for population growth. In particular, there is a need for the development of robust guidelines for fisheries management that would provide an acceptable probability of population growth given the inherent biological productivity of the stock (and its variability), the imprecision of forecasts and fisheries management, and a target growth rate required to meet persistence criteria.

Nonetheless, the recovery of populations is by no means certain even after known threats are reduced or eliminated, and the probability of a failure to recover may be related to the extent of the decline (Hutchings 2001). Larger recovery targets than those identified by the recovery plan may be desirable to increase the likelihood that populations can persist over the long-term in the face of this uncertainty.

Finally, measurable, objective recovery targets are only effective if there are programs in place to evaluate the status of the population and its habitat in relation to the recovery goals. Recovery plans should have an explicit link between recovery objectives, an evaluation cycle and the monitoring activities required to make those evaluations, although many do not (Campbell et al. 2002). While elements of these are contained in the three salmon recovery plans, there may be value in more explicitly linking monitoring activities to the objectives to highlight their central importance to the recovery process.

References:

Allendorf, F.W. and N. Ryman. 2002. The role of genetics in PVA. Pp. 50-85 in S.R. Beissinger and D.R. McCullough eds. Population Viability Analysis. Chicago Univ. Press.

Botsford, L.W. and J.G. Brittnacher. 1998. Viability of Sacramento River winter-run chinook salmon. Cons. Biol. 12:65-79.

Bradford, M.J. and J.R. Irvine. 2000. Land use, fishing, climate change and the decline of Thompson River, British Columbia coho salmon. Can.J. Fish. Aquat. Sci. 57:13-16.

Caughley, G. 1994. Directions in conservation biology. J. Anim. Ecol. 63:215-244.

Campbell, S.P. and 7 coauthors. 2002. An assessment of monitoring efforts in endangered species recovery plans. Ecol. Appl. 12:674-781.

Coltman, D.W., J.G. Piikington, J.A. Smith, and J.M. Pemberton. 1999. Parasite-mediated selection against inbred Soay sheep in a free-living, island population. Evolution 53:1259-1267.

COSEWIC 2003. COSEWIC assessment and status report on the sockeye salmon (Cultus population) in Canada. COSEWIC Ottawa, ix + 57pp.

Crnokrak, P., and D.A. Roff. 1999. Inbreeding depression in the wild. Heredity 83:260-270.

Cuenco, M.L., T.W.H. Backman, and P.R. Mundy. 1993. The use of supplementation to aid in natural stock restorstoration. Pp. 269-288 *In*: J.G. Cloud and G.H. Thorgaard (ed.) Genetic Conservation of Salmonid Fishes, Plenum Press, New York.

Elphick, C.S., J.M. Reed and J.M. Bonta. 2001. Correlates of population recovery goals in endangered birds. Cons. Biol. 15:1285-1291.

Emlen, J.M. 1995. Population viability of the Snake River chinook salmon. Can. J. Fish. Aquat. Sci. 52:1442-1448.

Ford, M.J. 2002. Selection in captivity during supportive breeding may reduce fitness in the wild. Conserv. Biol. 16:815-825.

Frankham, R. 1995a. Inbreeding and extinction: a threshold effect. Conserv. Biol.9:792-799.

Frankham, R. 1995b. Effective population size/adult population size ratios in wildlife: a review. Genet. Res. 66:95-107.

Frankham, R., J.D. Ballou, and D.A. Briscoe. 2002. Introduction to Conservation Genetics. Cambridge Univ. Press, Cambridge, 617 p.

Frankham, R. and I.R. Franklin. 1998. How large must a population be to retain evolutionary potential. Anim Conserv. 1: 69-73.

Franklin, I.R. 1980. Evolutionary change in small populations. Pp. 135-149 in M.E. Soule and B.A. Wilcox eds. Conservation Biology: an Evolutionary-Ecological Perspective. Sinauer.

Gross, M.R., and C.T. Robertson. 2004. Update COSEWIC status report on Atlantic salmon, Inner Bay of Fundy populations (*Salmo salar*). 44 p. (Unpublished interim report available from M. Gross, Univ. of Toronto)

Heath, D.D., C. Busch, J. Kelly, and D.Y. Atagi. 2002. Temporal change in genetic structure and effective population size in steelhead trout (*Oncorhynchus mykiss*). Mol. Ecol. 11:197-214.

Holling, C.S. 1959. The components of predation as revealed by a study of small mammal predation of the European pine sawfly. Can. Entomol. 91:385-398.

Hill, M.F., A. Hastings and L.W. Botsford. 2002. The effects of small dispersal rates on extinction times in structured metapopulation models. Am. Nat. 160:389-402.

Hutchings, J.A. 2001. Conservation biology of marine fishes: perceptions and caveats regarding assignment of extinction risk. Can. J. Fish. Aquat. Sci. 58:108-121.

Irvine, J.R. 2002. COSEWIC status report on the coho salmon, *Oncorhynchus kisutch* (Interior Fraser population) in Canada. In COSEWIC assessment and status report on the coho salmon, *Oncorhynchus kisutch* (Interior Fraser population) in Canada. COSEWIC viii+34 pp. Ottawa.

Irvine, J.R. and 7 coauthors. 2000. Stock status and genetics of interior Fraser coho salmon. CSAS Res. Doc. 2000-125.

Kapuscinski, A.R.D., and J.E. Lannan. 1984. Application of a conceptual model for managing Pacific salmon fisheries. Aquacult.43:135-146.

Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophies. Amer. Nat. 142:911-927.

Lande, R. 1995. Mutation and conservation. Cons. Biol. 9:782-792.

Lande, R., S. Engen, and B. Saether. 2003. Stochastic population dynamics in ecology and conservation. Oxford Series in Ecology and Evolution.

Larkin, P.A. 1980. A perspective on population genetics and salmon management. Can. J. Fish. Aquat Sci. 38:1469-1475.

Liermann, M. and R. Hilborn. 2001. Depensation: evidence, models and implications. Fish and fisheries 2:33-58.

Lynch, M. and R. Lande. 1998. The critical effective size for a genetically secure population. Anim. Conserv. 1:70-72.

Lynch, M., and M. O'Hely. 2001. Captive breeding and the genetic fitness of natural populations. Conserv. Gen. 2:363-378.

McElhany, P., M.H. Ruckelhaus, M.J. Ford. T.C. Wainwright and E.P. Bjorkstedt. 2000. Viable salmon populations and the recovery of evolutionary significant units. NOAA Tech. Memo. NMFS-NWFSC-42

Mills, L.S. and F.W. Allendorf. 1996. The one-migrant-per-generation rule in conservation and management. Cons. Biol. 10:1509-1518.

Morris, W.F. and D.F. Doak. 2003. Quantitative conservation biology. Sinauer Assoc.

Nickelson, T.E. and P.W. Lawson. 1998. Population viability of coho salmon, in Oregon coastal streams: application of a habtiat-based life cycle model. Can. J. Fish. Aquat. Sci. 55:2383-2392.

Peterman, R.M. and M. Gatto. 1978. Estimation of functional responses of predators on juvenile salmon. J. Fish. Res. Board 35:797-808.

Ratner, S., R. Lande, and B.B. Roper. 1997. Population viability analysis of spring chinook salmon in the south Umpqua River, Oregon. Cons. Biol. 11:879-889.

Reed, D.H., J.J. O'grady, B.W. Brook, J.D. Ballou and R. Frankham. 2003. Estimates of minimum viable population sizes for vertebrates and factors influencing those estimates. Biol. Cons. 11:23-34.

Reed, J.M. and 8 coauthors. 2002. Emerging issues in population viability analysis. Cons. Biol. 16:7-19.

Reisenbichler, R.R., and S.P. Rubin. 1999. Genetic changes from aritificial propagation of Pacific salmon affect the productivity and viability of supplemented populations. ICES J. Mar. Sci. 56:459-466.

Ricker, W.E. 1941. The consumption of young sockeye salmon by predaceous fish. J. Fish. Res. Board. Can. 5:293-313.

Ruggerone, G.T. and D.E. Rogers. 1978. Arctic char predation on sockeye salmon smolts at Little Togiak River, Alaska. Fish. Bull. 82:401-410.

Ryman, N., P.E. Jorde, and L. Laikre. 1995. Supportive breeding and variance effective population size. Conser. Biol. 9:1619-1628.

Ryman, N., and L. Laikre. 1991. Effects of supportive breeding on the genetically effective population size. Conserv. Biol. 5:325-329.

Saccheri, I., M. Kuussaari, M. Kankare, P. Vikman, W. Fortelius and I. Hanski. 1998. Inbreeding and extinction in a butterfly metapopulation. Nature 392:491-494.

Schubert, N.D. and 13 coauthors. 2002. Status of Cultus Lake sockeye salmon. CSAS Res. Doc. 2002/064

Soule, M.E. 2002. Foreward: raising the bar. Pp. ix-xi in S.R. Beissinger and D.R. McCullough eds. Population Viability Analysis. Chicago Univ. Press.

Taylor, A. 2003. Assessing the consequences of inbreeding for population fitness: past challenges and future prospects. Pp. 67-81 in Holt, W.V. et al. (eds.). Reproductive Science and Integrated Conservation. Cambidge Univ. Press.

Tear, T.H., J.M. Scott, P.H. Haywood and B. Griffith. 1993. Status and prospects for the success of the Endangered Species Act: a look at recovery plans. Science 262:976-977.

Tear, T.H., J.M Scott, P.H. Haywood and B Griffith. 1995. Recovery plans and the Endangered Species Act: are criticisms supported by data? Cons. Biol. 9:182-195.

Waples, R.S. 1990. Conservation genetics of Pacific salmon: 2, effective population size and the rate of loss of genetic variability. J. Heredity 81:267-276.

Waples, R.S. 2002a. Definition of estimation of effective population size in the conservation of endangered species. Pp 147-168 in S.R. Beissinger and D.R. McCullough eds. Population Viability Analysis. Chicago Univ. Press.

Waples, R.S. 2002b. Effective size of fluctuating salmon populations. Genetics 161:783-791.

Waples, R.S. 2004. Salmonid insights into effective population size. Pp 296 to 319 in: A.P. Hendry and S.C. Strearns (eds). Evolution Illuminated. Oxford Univ. Press.

Waples, R.S., and C. Do. 1994. Genetic risk associated with supplementation of Pacific salmonids: captive broodstock programs. Can. J. Fish. Aquat. Sci. 51:310-329.

Wohlfarth, G.W. 1993. Genetic management of natural fish populations pp. 227-230 *In*: J.G. Cloud and G.H. Thorgaard (ed.) Genetic Conservation of Salmonid Fishes, Plenum Press, New York.

Wood, C.C. 1987. Predation of juvenile Pacific salmon by the common merganser (*Mergus merganser*) on eastern Vancouver Island. I: Predation of seaward-migrating juvenile salmon. Can. J. Fish. Aquat. Sci. 44:941-949.

Wood, C.C., and L.B. Holtby. 1998. Defining conservation units for Pacific salmon using genetic survey data. p. 233-250 *In*: B. Harvey, C. Ross, D. Greer, and J. Carolsfeld (ed.). Action Before Extinction: An International Conference on Conservation of Fish Genetic Diversity. World Fisheries Trust, Victoria, Canada

Wright, S. 1931. Evolution in Mendelian populations. Genetics 16:97-159.

Appendix A.

Recovery Goals and Objectives excerpted from the September, 2004 draft recovery plans for Cultus Lake and Sakinaw Lake sockeye salmon and Interior Fraser coho salmon.

Cultus Lake Sockeye Salmon

Recovery Goal

Our goal is to halt the decline of the Cultus sockeye population and to return it to the status of a viable, self-sustaining and genetically robust wild population that will contribute to its ecosystems and have the potential to support sustainable use.

Recovery Objectives

We identify four objectives that are sequential steps toward the recovery of the population. Objective 1 secures genetic variability, Objective 2 ensures the population is growing, and Objective 3 achieves delisting by COSEWIC – the change in designation from *Endangered* to *Not at Risk*.

Once the population is delisted, conservation objectives should be consistent with (*i.e.*, not less than) those specified for other sockeye populations. We make the assumption that conservation benchmarks will be defined in DFO's Wild Salmon Policy. Objective 4 proposes candidate benchmarks that have been discussed in consultations on the draft Wild Salmon Policy and correspond to our current understanding of the dynamics of Cultus sockeye.

Progress toward achieving all four objectives will be assessed annually by engaging local communities through workshops, websites and other media, and recommending further studies required to address knowledge gaps.

Objective 1. Ensure the genetic integrity of the population by exceeding a four-year arithmetic mean of 1,000 successful adult spawners with no fewer than 500 successful adult spawners on any one cycle.

Notes: A *successful spawner* is one that fertilizes eggs (male) or deposits eggs (female). The number of successful spawners is based on fence counts and carcass recoveries from spawning ground surveys in the lake. Because success among males cannot readily be determined from the carcasses, the estimate of female success is applied to the entire population.

The genetic consequences of small populations include the random loss of genetic and phenotypic variation and the loss of evolutionary potential associated with a reduction in genetic diversity (Allendorf and Ryman 2002). To avoid negative genetic impacts, population abundance must be maintained above the *minimum* genetically effective population size of 1,000 per generation. Applying conventional assumptions (Waples 2002) to the life history of Cultus sockeye, this implies that the average annual spawning abundance should exceed 1,000 fish, with no fewer than 500 spawners in any one year.

How do the adults produced by captive breeding figure in this total? The number of successful Cultus sockeye spawners in any given year is deemed to include all naturally spawning sockeye, including the progeny of captive broodstock that have survived in the

wild since their release as juveniles. However, adults collected as broodstock for artificial propagation will not be included in the estimate of successful spawners produced for that year.

Although the target levels in Objective 1 eliminate genetic risk to the population (preserve genetic resources) and are adequate to avert listing under IUCN Criterion D, they are not adequate to avert listing under criteria A or C unless population abundance is increasing. Delisting should be assured by meeting the following objective (Objective 2).

Objective 2. Ensure growth of the successful adult spawner population for each generation (that is, across four years relative to the previous four years), and on each cycle (relative to its brood year) for not less than three out of four consecutive years.

Notes: The time series of spawner abundance information shows that generation size rarely increases unless there is cycle over cycle growth (*e.g.*, 1994 is bigger than 1990) on at least three of the four cycles. Historical records from 1930 to 2003 show a generation growth rate of 54% when growth occurred in three out of four years. Given the uncertainties in forecasts and in-season processes, managers should target growth on *all* cycles during the recovery phase to increase their likelihood of achieving positive generation-over-generation growth. If one or more of the previous three years declines, more stringent measures will be required to ensure positive growth in the current year. A numeric target for population size and a time frame for achieving it would permit recovery implementation groups to establish growth rate targets for the population.

Objective 3. Recover the population to the level of abundance at which it can be delisted (*i.e.*, designated *Not at Risk*) by COSEWIC.

Notes: COSEWIC uses the quantitative IUCN criteria as guidelines to assess the status of wildlife species in Canada. Because the IUCN criteria are not always appropriate for regional (*versus* global) application, COSEWIC also considers other biological characteristics and threats when designating species status. We acknowledge that such assessments and designations are COSEWIC's mandate. Here we provide advice for future COSEWIC reassessments in the context of the recovery goal for Cultus sockeye. For this population to be recovered, the following questions will have affirmative answers:

- *Have objectives 1 and 2 been achieved?* A recovered population must exceed the minimum abundances identified in Objective 1 and must have shown the growth in successive generations identified in Objective 2.

- *Have the causes of the decline identified by COSEWIC been addressed?* The COSEWIC status report identifies three principal causes: *over-exploitation in fisheries, recruitment failure* and *high pre-spawn mortality*. Regulatory agencies must develop short and long term management plans that include harvest rules and escapement policies for the sustainable use of Cultus sockeye. These plans must be consistent with the Team's goal and objectives and explicitly address uncertainties in population dynamics and management imprecision while protecting the population

from unanticipated catastrophic PSM. The population must be able to withstand at least one cycle of poor environmental conditions without declining to a generation average of less than 1,000 successful spawners and 500 successful spawners on any cycle. This means managers must deliver a big enough escapement to the counting fence to achieve these population sizes on the spawning grounds. To do so, they must consider forecasting and in-season run size errors as well as uncertainty about PSM. For example, Objective 1 could be achieved despite 93% PSM (the most extreme ever observed) provided the management plan delivered an escapement of no fewer than 7,100 adults to the fence.

- *Is freshwater productivity adequate to support recovery?* Analysis of historical data provides some evidence that, when spawner abundance is less than about 7,000 fish, freshwater productivity is lower (20-30 smolts/spawner) than in years of higher abundances (>60 smolts/spawner; see *Biological Limiting Factors*). The low productivity at current abundances will limit the population's potential for recovery or sustainable use. An increase in productivity as the population recovers is, therefore, an important indicator of recovery.

- *Have emergency mitigative measures been relaxed?* A recovered wild population would safely allow stopping supplementation and thereby eliminate it as a source of genetic risk. A recovered population in its natural ecosystem would not require ongoing predator control measures. We note, however, that the productivity of predator populations may have increased as a result of the invasion of Eurasian watermilfoil. Consequently, plant or predator removal may need to continue.

Objective 4 (long term objective). Recover the population to a level of abundance (beyond that of Objective 3) that will support ecosystem function and sustainable use.

Notes: This objective addresses ecosystem and sustainable use goals. Choosing an appropriate level of abundance requires the weighing of scientific advice in the context of broad policy objectives for salmon management which often must consider conflicting societal values. This target level of abundance must reflect the unique characteristics of the Cultus population and its ecosystems, *i.e.*, represent some reasonable proportion of the population's productive capacity. Setting the target level of abundance is beyond the Team's mandate and should be addressed by government policy-makers in consultation with the stakeholders. It is expected that the DFO's Wild Salmon Policy, to be released in 2005, will provide an appropriate framework.

The choice of a long-term target level of abundance must be based on our current understanding of the production dynamics of the Cultus population. Potential reference points include the following benchmarks, all of which are described in detail in Annex 2:

- The abundance providing maximum sustainable yield (S_{MSY}) or some proportion of S_{MSY};
- Some proportion of the productive capacity of the lake;
- Historic abundance; and
- The abundance at which ecosystem function is maintained.

Sakinaw Lake Sockeye Salmon

Recovery Goal

The goal is to stop the decline of the Sakinaw Lake sockeye salmon population and re-establish a self-sustaining, naturally spawning population, ensuring the preservation of the unique biological characteristics of this population.

Recovery Objectives

1. **Inform the local community and other stakeholders about the recovery planning process for Sakinaw sockeye and encourage them to become involved in the stewardship of the Sakinaw Lake watershed.**

   This recovery strategy is intended to promote the health of the Sakinaw Lake watershed both as an end in itself and to maintain long-term viability of Sakinaw sockeye. Community and stakeholder initiatives and support for stewardship activities will be critical to the success of the recovery process.

2. **Achieve continued growth in the generational average by increasing spawner abundance relative to the brood year (4 years prior) for at least 3 out of 4 consecutive years.**

   A positive overall population trajectory is required to demonstrate population viability and to meet criteria for delisting by COSEWIC. Management planning must attempt to achieve positive sockeye population growth in all years during the recovery phase. More stringent measures must be considered to ensure positive growth in the current year whenever one or more of the three preceding years has shown a decline relative to its brood year, four years prior. Extreme management efforts are required in 2004 and 2005, because annual spawner abundance has declined continuously since 2000 and because 2005 is the last opportunity to take advantage of significant adult returns expected form previous fry supplementation efforts.

3. **Increase the annual number of spawners[2] (here including those removed for hatchery broodstock) to no fewer than 500 from 2004 to 2007.**

   The recovery team emphasizes the urgent need to safeguard genetic diversity by increasing adult sockeye escapements, but also recognizes limits to the biological feasibility of attaining adequate spawning abundance in the immediate future. Accordingly, the team has identified two interim objectives (3 and 4) that appear biologically feasible. The first interim objective is to attempt to recover the population to a minimum of 500 adults in a fast and effective manner, by relying heavily on intensive fish culture initiated in 2000 and continuing into 2002 including the establishment of a captive brood program. The first interim target will include all adults that survive to reach the spawning beaches in spawning condition, including those brood removed for artificial propagation for fry supplementation and the captive brood program. Efforts to maximize genetic diversity and to minimize in-breeding are in place and are described in Appendix 2.

   Achieving this objective will also depend on minimizing mortality wherever possible, e.g. fishing mortality and juvenile and adult predation.

4. **Increase the number of naturally[3] produced spawners to no fewer than 500 annually in 2008 to 2011.**

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[2] Healthy mature fish attempting to spawn naturally in Sakinaw Lake, but excluding non-anadromous fish (pending resolution of their identity).

[3] Spawned and reared in natural fish habitat; not released from a hatchery

The second interim objective is intended to maintain focus on recovery of a self-sustaining population that is "wild" by nature. This interim target of 500 by 2008 will include only naturally produced adults that spawn naturally within the lake. It is expected that brood collection ands subsequent fish culture activities will stop and all returning adults will remain within Sakinaw Lake to spawn under their own volition. This objective will be achieved through earlier efforts to rebuild using intensive fish culture, rehabilitation of critical habitats, management strategies implemented to reduce interception and community and stakeholder efforts in stewardship activities.

5. **Ensure that by 2017, the mean population abundance in any four year period exceeds 1,000 naturally produced spawners, with no fewer than 500 naturally produced spawners in a year.**

   This level has been judged the minimum viable population (MVP) size required to prevent the random loss of genetic diversity, and consequent loss of viability and evolutionary potential...

6. **Identify, assess, protect and where necessary, rehabilitate habitats critical to the recovery goal.**

   Salmon population declines in many areas of the Pacific Northwest are attributed to habitat degradation. In Sakinaw Lake, with the exception of the outlet stream, little information exists on the important and critical habitats required by the sockeye population. Habitat degradation and loss has probably caused a decline in the productivity of the Sakinaw sockeye population. Regardless, in order to sustain any future recovered population sufficient suitable habitat must be available to the population. Research, governance and stewardship methods will be necessary to achieve this.

7. **Identify the level of abundance required to support ecosystem function and sustainable use, as a longer-term target for recovery.**

   This objective is intended to address long-term goals and sustainable use. Biological benchmarks or milestones will be determined based on an understanding of the population dynamics of Sakinaw sockeye and the productive capacity of the Sakinaw Lake ecosystem. The following candidate benchmarks have been suggested for Cultus sockeye and are considered equally relevant to Sakinaw sockeye:

- The number of spawners yet to be determined that would provide maximum sustainable yield (S_{MSY});
- The number of spawners required to "seed" the lake above some minimum proportion of its productive capacity;
- The average number of spawners observed historically before the run collapsed. The average escapement between 1957 and 1987 was approximately 5000 spawners;
- The number of spawners considered sufficient to maintain ecosystem function (not yet defined).

Interior Fraser Coho Salmon

Recovery Goal

The recovery goal is to secure the long term viability and diversity of naturally spawning coho salmon within the Interior Fraser River watershed.

Recovery Principles

The Interior Fraser River region is a vast and varied watershed, and coho salmon are found at different levels of abundance throughout it. Part of the evolutionary legacy of Interior Fraser Coho is the biodiversity within the coho salmon in this watershed area. This diversity is expressed as variation in neutral alleles, and as quantitative and qualitative observations of diversity in life history traits such as adult migration timing, fecundity, and body size. This diversity of adaptations is the basis for the continued production and survival of populations and species, and hence their ability to adapt to change, and to withstand harvest.

To guide the development of recovery objectives, three principles apply:

- *Principle 1: The recovery of Interior Fraser Coho will require the maintenance of sufficient levels of abundance and spatial diversity to achieve the recovery goal.*

Recovery will not be achieved by having one large spawning aggregation while allowing the remainder to be extirpated, nor does it necessarily mean large abundances of fish in every stream that historically may have had coho salmon. The challenge is to determine the appropriate levels of abundance and distribution that that will satisfy this first principle.

- *Principle 2: The spatial structure and distribution of Interior Fraser Coho will be considered at the level of populations and sub-populations.*

Populations are defined as genetically differentiated units identified through the analysis of neutral allele frequencies. Five populations have been identified that correspond to major drainage basins within the Interior Fraser River watershed (see section 1.4). Within each of these populations coho salmon interbreed to varying degrees but the populations are sufficiently isolated from each other that there will be persistent adaptations to the local habitat and limited exchange or migration amongst them.

One or more sub-populations have been identified within each of the five populations (Section 1.4). Sub-populations are considered to be demographically independent units, that is, their population dynamics or probability of persistence is independent of events in adjacent sub-populations. Migrations may occur among sub-populations that reduce the opportunities for genetic differentiation, but they would be relatively limited in scope. Procedures for defining sub-populations are inexact and the relevant data are scarce; some of the factors that have been considered include genetic and phenotypic differentiation, independence in trends in abundance, estimates of straying or interchange, and habitat and ecological considerations.

Most sub-populations contain many spawning aggregations or demes. Demes are groups of fish found reproducing within a single stream or portion of a stream. Observations of the year to year variation in the distribution of spawners, and the straying of marked fish among streams suggests that considerable interchange can occur among nearby natal streams; thus, demes are not necessarily persistent features of a population's structure. Therefore, the preservation of all demes is not considered a prerequisite for the recovery of Interior Fraser Coho.

- *Principle 3: The recovery goal is considered achieved when there are one or more viable sub-populations in each of the five populations.*

This principle is designed to ensure that there is representation from each of the five genetically distinct populations of Interior Fraser Coho. Ensuring that more than one sub-population is viable within a population is desirable as it insures against catastrophic events, and would likely lead to protection of a greater proportion of the biodiversity of a population.

The term viable in Principle 3 means that the abundance and productivity (as affected by the combination of freshwater and marine habitat conditions, and fishing mortality) of the sub-population are sufficient for it to persist over the long-term. Viability is achieved by establishing minimum population levels and by ensuring that habitat conditions and fishing mortality are adequate to sustain long-term productivity.

A provisional operational rule for application of Principle 3 is that within each of the 5 populations, at least half of the sub-populations must be viable. This means that for the North and South Thompson populations, 2 of the 3 sub-populations within each must be viable, 1 of the 2 sub-populations in each of the Upper Fraser and Lower Thompson populations must be viable, and the single sub-population within the Fraser Canyon population must be viable.

Recovery Objectives

The following objectives need to be achieved in order for Interior Fraser Coho to be considered to have met the recovery goal.

OBJECTIVE 1: The 3-year average escapement in at least half of the sub-populations within each of the five populations is to exceed 1,000 naturally spawning coho salmon, excluding hatchery fish spawning in the wild. This objective is designed to provide the abundance and diversity required to satisfy the Recovery Goal.

Note: If the historical patterns of distribution within the Interior Fraser River watershed continue into the future, this objective will be achieved when the escapement to the designated unit is at least 20,000 to 25,000 wild spawners (see section 3.4.3).

OBJECTIVE 2: Maintain the productivity of Interior Fraser Coho so that recovery can be sustained. This objective is designed to ensure that the threats to recovery are addressed.

This objective may be met by addressing the causes for the decline that were identified by COSEWIC:

- Development of a harvest management plan to ensure that exploitation rates are appropriate to changes in productivity caused, for example, by fluctuations in ocean conditions.
- Identification, protection, and if necessary rehabilitation of critical and important habitats.
- Ensure that the use of fish culture methods is consistent with the recovery goal.

POSSIBLE LONGER TERM OBJECTIVES: Over the long term it may be desirable to recover Interior Fraser Coho so that other societal objectives can be achieved. These objectives are within the scope of the recovery goal, but are beyond the mandate of the Interior Fraser Coho Recovery Team. Examples of possible long term goals include:

- To achieve three year average escapements in all sub-populations within each of the five populations exceeding 1,000 naturally spawning coho salmon (excluding hatchery fish spawning in natural habitats).
- To recover each of the five populations to the maximum sustainable yield (MSY) abundance level, *i.e.* to the Green Zone in Figure 21.
- To recover each of the five populations to their maximum historic abundance levels.
- To recover to a level where the freshwater productive capacity within each of the five populations is optimized. A possible approach would be to estimate the maximum capacity as smolts/km and apply this to the designated unit.
- To increase adult returns so that sufficient marine origin nutrients enter each population to optimize ecosystem function.
- To recover to a level that will allow for harvesting at higher levels than are currently allowed; including, but not limited to, terminal area (i.e., in estuary or freshwater areas near natal streams) harvesting for consumptive and non-consumptive purposes.